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Pollen Grain Morphology and Its Taxonomic Significance in the Amherstieae, Cynometreae, and Sclerolobieae (Caesalpiniaceae) with Special Reference to American Genera

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INTRODUCTION

The Leguminosae made up of trees, shrubs, and herbs represent one of the three largest families of Angiosperms. It consists of about 350 genera and approximately 13,000 species and is divided into three subfamilies: Mimosoideae, Caesalpinioideae, and Lotoideae. Some authors choose to treat the Leguminosae as a single order composed of three families: Mimosaceae, Caesalpiniaceae, and Papilionaceae, a classification accepted in this paper.

As presently defined, the Caesalpiniaceae comprise about 135 genera distributed among nine tribes: Cassieae, Bauhinieae, Dimorphandreae, Schwartzieae, Eucaesalpiniaceae, Kramerieae[1], Amherstieae, Cynometreae, and Sclerolobieae. The present investigation concerns the latter three tribes. These three arboreal tribes representing about 70 genera and 550 species are tropical in distribution. The Sclerolobieae are limited to the American tropics, whereas the Amherstieae and Cynometreae are pantropical in distribution.

The delimitation of three caesalpiniaceous tribes, the Amherstieae, Cynometreae, and Sclerolobieae is controversial. Various characters such as fusion or non-fusion of the ovary to the wall of the receptacle (Bentham, 1840; Taubert, 1892), the number of ovules (Harms, 1915) and the presence of valvate or non-valvate bracteoles in the bud (Leonard, 1957) have been suggested as key characters in the separation of the tribes Amherstieae and Cynometreae. Some workers have recommended the taxonomic fusion of the two tribes (Baker, 1930); others have suggested the fusion of all three tribes (Dwyer, 1954a).

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[1]Some authors treat the Kramerieae as a distinct family; others exclude it altogether from the legumes.

This palynological study was proposed as a possible means of determining more accurately the natural relationships among the genera of the three tribes. A study of the pollen in preference to a study of other characters seemed desirable for several reasons. First, pollen characters which are conservative, non-plastic characters are especially suited for investigations in higher plant groupings (Wodehouse, 1928). Secondly, very few of the pollen grains of the three tribes have been investigated. Tulasne (1845) included drawings of the pollen of *Diptychandra*, *Phyllocarpus*, and *Pterogyne* in the original descriptions of the genera. Erdtman (1952) in his pollen survey included the description of 12 species and F. G. Smith (1956) in his palynological study associated with bee botany in Tanganyika described grains of 12 species.

Thirdly, only two investigators, in very limited studies, have applied palynological data to taxonomic problems in the study of these genera. Noteworthy is Erdtman's (1955) study of the pollen of *Macrolobium* (Amherstieae) in which he found a significant difference in the pollen whereby the African species, now relegated to the recently revived genus *Anthonotha*, can be separated from the American species. Significant too is the study of Leonard (1957) in which he used the pollen description of F. G. Smith in suggesting some palynological relationships in a study of the African Amherstieae and Cynometreae.

Because of the limited amount of herbarium material of many of the genera, it was impossible for the author to obtain specimens representing every species of the three tribes. Specimens of 212 species representing 61 genera were obtained of the approximately 550 species distributed among 70 genera in the three tribes.

In this study special consideration is given to American genera since herbarium material of these is more readily obtainable. Seven New World genera were selected for detailed study because of their prominence in current taxonomic studies. These include: *Sclerolobium*, *Dicymbe* (Sclerolobieae) and *Tachigalia*, *Eperua*, *Brownea*, *Peltogyne*, and *Crudia* (Amherstieae).

ACKNOWLEDGMENT

The writer wishes to express her gratitude to Doctor John D. Dwyer of St. Louis University, who is studying this group of genera along classical taxonomic lines, for suggesting the problem, for supplying the herbarium material, and for furnishing advice and assistance while this study was in progress.

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Thanks are also due to the staff at the Missouri Botanical Library for allowing use of the facilities during this investigation.

MATERIALS AND METHODS

Hebarium material obtained from the following herbaria was used in the study:

Jardin Botanique de L'Etat, Bruxelles, Belgium (B)
Royal Botanical Garden, Edinburgh, Great Britain (E)
Chicago Natural History Museum, Chicago, Ill. (F)
Conservatoire et Jardins Botaniques, Geneva, Switzerland (G)
Missouri Botanical Garden, St. Louis, Mo. (MO)
New York Botanical Garden, New York, N.Y. (NY)
Museum National d'Histoire Naturelle, Paris, France (P)
Botanical Museum and Herbarium, Utrecht, Netherlands (U)
National Museum, Washington, D.C. (US)
Naturhistorisches Museum, Wien, Austria (W)
Herbarium at Yale University, New Haven, Conn. (Y)

For purposes of citation letters designating the particular institution are used.

The pollen-bearing parts, including the anthers and other parts to which the pollen was adhering, were removed from the flower specimens with the aid of a dissecting microscope. Whole mounts of pollen exines were prepared according to Erdtman's acetolysis procedure (1952).

Sections of the exines were made following a modification of Erdtman's (1957) technique for the cutting of ultra-thin sections. Lack of material made it impossible to prepare sections for every specimen. The acetolysed grains were washed with distilled water, dehydrated in ethyl alcohol, and infiltrated with a mixture of methyl and butyl methacrylate (in the proportions 6:1). The dehydration and infiltration of the exines were carried out in microcentrifuge tubes and centrifugation preceded each change of alcohol and methacrylate. The exines were then embedded in gelatine capsules (No. size 1) in the methacrylate mixture to which the catalyst benzoylperoxide had been added. Sections were cut at 1–2 μ with a glass knife fitted into a Spencer Rotary Microtome adapted for thin sectioning (Pease and Baker, 1948). Twelve to twenty sections were floated on a slide in 20% alcohol to which a few drops of Haupt's adhesive had been added.

The methacrylate was removed from the sections by immersion of the slides in acetone. Subsequently the sections were stained with safranin or iodine green, dehydrated, and mounted in canada balsam following the conventional methods of microscopical technique.

Measurements of pollen were made under the 97× oil immersion and 10× ocular with an ocular micrometer. The polar axis (P) and the equatorial axis (E) of each of fifty grains from each specimen studied were measured. The means of the polar axis and the equatorial axis were obtained. Means based on fewer than 50 measurements are indicated by an asterisk.

A shape ratio of the polar to the equatorial axis (P/E) was obtained for each grain measured. Means of the shape ratios were then used to place the pollen in one of the shape classes (Erdtman, 1952). In those grains marked by permanent tetrads with tetrahedral arrangement, measurements were made according to Cranwell (1953). One side and the altitude of the equatorial triangle, which forms a side of the tetrahedron formed by the pollen tetrad, were measured. These measurements are designated as side a and h_a, respectively.

Measurements of sculptural elements, lumina, and verrucae were made under the 97× oil immersion objective and 25× ocular fitted with an ocular micrometer. In heterobrochate reticulate grains, the largest lumen apparent in equatorial view was measured along its long axis. The muri surrounding the lumen were included in the measurement unless the muri were very wide. They were then measured separately. Ten measurements were taken and the mean was determined. Each of these measurements was made on a different grain. The verrucae in polar view were measured along the long axes.

KEY TO GLYPHS

<u>Reticulate</u>

Lumina size 7-18 μ

Lumina size ca. 7 μ

Lumina size > 2 u < 7 μ

Lumina size < 2 μ

Sexine pattern more pronounced in mesocolpia

Sexine uniform over grain surface

Clavate, long wide colpi

Psilate brevicolpi

Psilate, long, narrow colpi

Lolongate ora

Lalongate or spherical ora

<u>Psilate</u>

Densely packed long bacula

Thin sexine

<u>Verrucate</u>

Large verrucae

Small verrucae

Crassimarginate

Not crassimarginate

<u>Striate</u>

Long lirae

Short fragmented lirae

Narrow twisting lirae

<u>Rugulate</u>

<u>Ornate</u>

<u>Clavate baculate</u>

<u>Retipilate</u>

Two grains falling on the same point

Description of the pollen follows the terminology proposed by Erdtman (1952) and, to a lesser degree, Faegri and Iversen (1950). Drawings were made with the aid of a camera lucida. The grains are usually presented in equatorial view in the palynograms (Plates 1–6) and a small drawing representing the opposite view of the main figure is shown in the lower right corner. Square figures providing the results of an LO analysis and drawings of ultra-thin sections at a higher magnification than the main figure are presented at the right.

Pictorialized scatter diagrams were used in analyzing the relationships among the pollen types in sexine pattern, colpi and ora characters, and in size and shape of pollen. The method used is based on a modification of Anderson's (1954) technique. The polar axis (P) is plotted on the ordinate and the equatorial (E) axis on the abscissa.

A uniform set of glyphs is used throughout the scatter diagrams (cf. Key to Glyphs, p. 158). Since the sculpturing of pollen has been found by most investigators to be a very constant and hence taxonomically important character, the circle of the glyph, a rather prominent part of the symbol was variously modified to represent the eight sexine patterns found in the pollen. Retipilate and ornate sexines, both closely related to the reticulate, are indicated by small changes in the reticulate symbol. Likewise, the rugulate, a modified striate type, has been given a symbol much like that of the striate.

Within each sculptural group various characters differentiate several types. These characters are illustrated by modifying the point at which the ray originates from the circle. Varying lengths of rays represent variations within the same character. Thus a long ray without a dot, the half ray, and the lack of a ray indicate progressive reduction of lumen size.

In order to determine the efficiency of the pictorialized scatter diagram in portraying differences in pollen size in this study, the range of variation in P and E was investigated in ten randomly selected pollen types (Fig. 1). The 100 measurements (50 P and 50 E) of each selected type are plotted in Fig. 1. A line drawn to include the 50 points indicates the limits of the range. The mean of each P and E, the only points used on the pictorialized scatter diagram, is likewise indicated in Fig. 1. From this investigation it seemed likely that since the size range is somewhat small, moderate differences in size of pollen indicated on a scatter diagram in this study can be interpreted as significant. Certainly scatter diagrams can be used effectively in a study such as this where only trends and relationships of pollen size are sought.

The pollen descriptions are presented in alphabetical order of the genera which are grouped into the three tribes. Capitaine's (1912) scheme of the tribes is used since this is the latest work in which all three tribes are considered as individual taxa and in which both African and American genera are included. Twelve genera studied in this investigation were not included in Capitaine's study (1912). Here these twelve genera are placed in the tribes to which they were assigned by their respective authors except *Sindora* Miq. De Wit (1949) recently monographed *Sindora* placing it with the Amherstieae although it had been assigned to the Cynometreae since Bentham's time (1865). It is here placed in the Amherstieae.

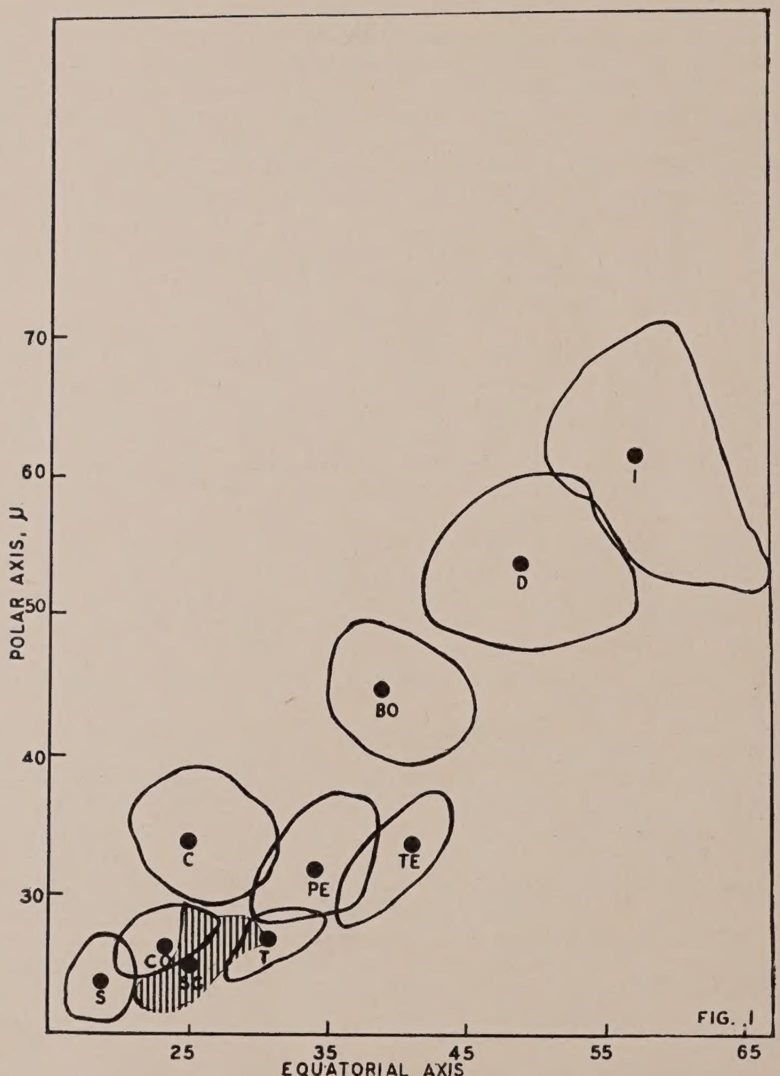


FIG. 1. Range of variation in the polar (P) and equatorial (E) axes of the pollen of 10 species selected at random from the 212 species studied in this investigation. A point indicates the mean of P and E of each selected pollen type; a line enclosing the point denotes the range of variation. BO, *Brownea similis, Maguire & Polite 28968A (NY)*; C, *Crudia tomentosa, Froes 1493*; CO, *Copaifera mildbraedii* Harms, *Louis 29666 (US)*; I, *Intsia bijuga, R. S. Williams 2738 (NY)*; PE, *Peltogyne gracilipes, Ducke 35181*; S, *Sclerolobium eriopetalum, Ducke 24296*; SC, *Scorodophloeus zenkeri, Zenker 2245 (P)*; T, *Tachigalia rusbyi, Tutin 201 (US)*; TE, *Tessmannia yangambiensis, Louis 1011 (US)*.

The generic palynological descriptions include the shape classes of the pollen, sculptural characteristics, and features of the ora and colpi. The specific differences follow and include the shape class, the P X E value and the P/E ratio. Differences in sculpturing are also noted in grains where this occurred.

Keys to the genera based on pollen characters were prepared.

RESULTS AND DISCUSSION

Description of the Pollen

Sclerolobieae

Batesia Spruce—Grains are 3-colporate, oblate spheroidal, colpi long and narrow, ora varying in shape from rectangular to elliptical or spherical, sexine reticulate, lumina measuring ca. 1–2 μ, polygonal lumina, heterobrochate.

Batesia floribunda Spruce ex Benth., *Ducke 1699* (*MO*)—Plate I, 6.
Oblate spheroidal, 24×26 μ, (P/E = 0.95).

Campsiandra Benth.—Grains are 3-colporate, oblate spheroidal, colpi long and narrow, ora varying from rectangular to spherical or elliptical, sexine psilate.

Campsiandra angustifolia Spruce ex Benth., *Klug 1196* (*F*).
Oblate spheroidal, 35×37 μ, (P/E = 0.95).
C. angustifolia, *Spruce 2561* (*F*).
Oblate spheroidal, 32×35 μ, (P/E = 0.91).
Campsiandra comosa var. *laurifolia* (Benth.) Cowan, *Wurdack* and *Monachino 39787* (*US*)—Plate 1, 2.
C. comosa, *Sandwith 220* (*NY*).
Oblate spheroidal, 27×30 μ, (P/E = 0.90).
C. comosa, *Luetzelburg 2461* (*NY*).
Prolate spheroidal, 42×41 μ, (P/E = 1.01).
Campsiandra laurifolia Benth., *Spruce s. n.* (*F*).
Oblate spheroidal, 39×40 μ, (P/E = 0.98).
C. laurifolia, *Krukoff 5897a* (*F*).
Prolate spheroidal, 38×38 μ, (P/E = 1.01).

Cenostigma Tul.—Grains are 3-colporate, suboblate, wide clavate colpi, ora elliptical lolongate, sexine coarsely reticulate, simplibaculate, heterobrochate with lumina sizes varying from 2.5–4.4 μ, sexine = $2 \times$ nexine. The bacula of the colpi are narrow and more closely spaced than those on the remainder of the grain surface. Very small capita terminate the colpi bacula.

Cenostigma macrophyllum Tul., *Dahlgren 973* (*F*).
Subolate, 48×58 μ, (P/E = 0.81), Lumina 4.1 μ.
C. macrophyllum, *Black*, *Pires*, and *Lima 54–16450* (*US*)—Plate 1, 11.
Suboblate, 43×54 μ, (P/E = 0.80), Lumina 2.5 μ.
Cenostigma tocantinum Ducke, *Ducke 15643*.
Suboblate, $36^* \times 49^*$ μ, (P/E = 0.75), Lumina 4.4 μ.
Cenostigma gardnerianum Tul., *Blanchet s. n.* (*MO*).
Suboblate, 48×58 μ, (P/E = 0.81), Lumina 4.4 μ.

Dicymbe Spruce ex Benth.—Grains are 3-colporate, shape varying from

oblate spheroidal, to subprolate, spherical ora, sexine pattern varying from rugulate to striate or verrucate, narrow psilate colpi.

Section *Dicymbe*

Dicymbe heteroxylon Ducke, *Ducke 1497* (*NY*).
Oblate spheroidal, 40×46 μ, (P/E=0.88), Striate sexine.
Dicymbe altsoni Sandwith, *Forest Department 5459* (*NY*)—Plate 1, 14.
Prolate spheroidal, 52×52 μ, (P/E=1.02), Striate sexine.
Dicymbe fraterna Cowan, *Pinkus 31* (*US*).
Oblate spheroidal, 49×53 μ, (P/E=0.93). Verrucate sexine with mural islands tending to be 2× as long as wide.
Dicymbe jenmani Sandwith, *Sandwith* and *Pinkus 31* (*F*).
Oblate spheroidal, 51×56 μ, (P/E=0.91). Verrucate with mural islands tending to be 2× as long as wide.

Section *Triplopetala*

Dicymbe amazonicum Ducke, *Ducke 312* (*US*).
Oblate spheroidal, 39×41 μ, (P/E=0.94). Sexine rugulate, mural strips long and narrow and often pointed tending to be arranged at angles to one another.
D. amazonicum, *Ducke 35091* (*NY*).
Oblate spheroidal, 39×43 μ, (P/E=0.92).

Section *Eremopetala*

Dicymbe froesii Ducke, *Froes 21372* (*NY*)—Plate 1, 12.
Subprolate, 45×38 μ, (P/E=1.17). Sexine rugulate, mural strips much longer than wide and arranged haphazardly often at angles to one another.
Dicymbe stipitata Cowan, *Cuatrecasas 7153* (*US*).
Subprolate, 39×34 μ, (P/E=1.16). Sexine striate with narrow lirae[2].

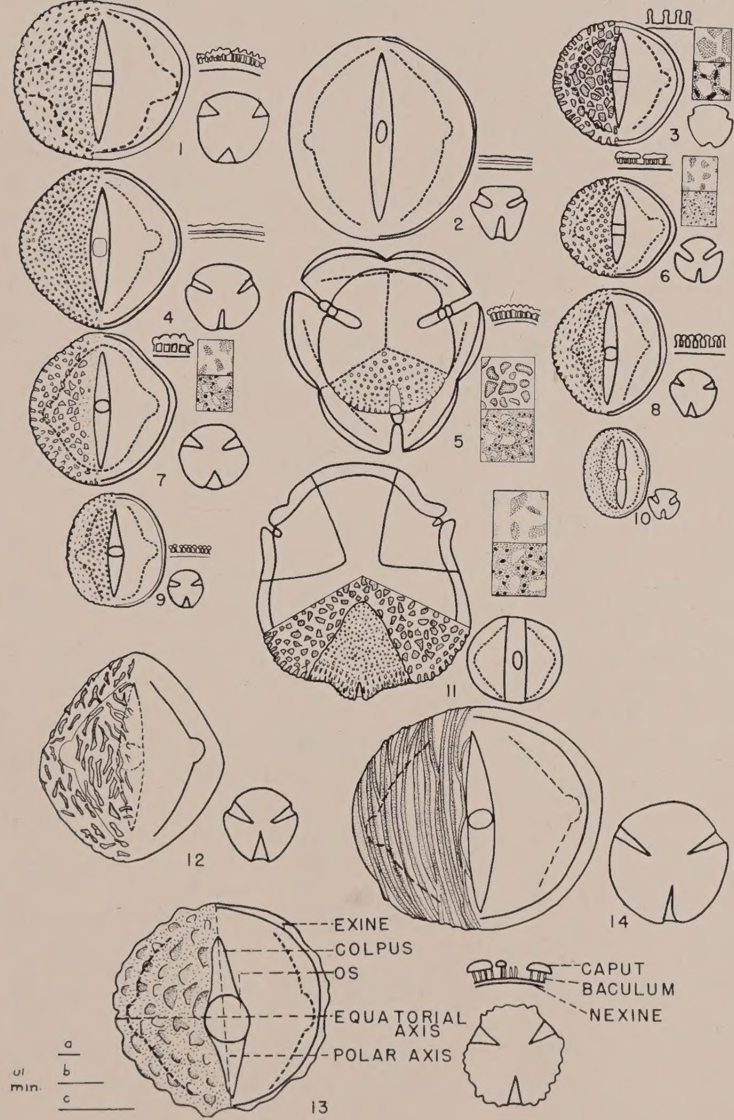
[2]The term lirae connotes the ridges in the striate pattern; whereas the striae indicate the grooves according to Erdtman (1952). Current usage of the term would often lead one to believe otherwise.

EXPLANATION OF PLATE I

PLATE 1.—Palynograms of the Sclerolobieae.—1. *Recordoxylon amazonicum* Ducke, *Maguire* and *Fanshawe 23050* (*MO*).—2. *Campsiandra comosa* var. *laurifolia* (Benth.) Cowan, *Wurdack* and *Monachino 39787* (*US*).—3. *Sclerolobium macrophyllum* Vogel, *St. Hilaire 597 B_1* (*F*).—4. *Phyllocarpus riedeleii* Tul., *Campos Portos 23623* (*US*).—5. *Diptychandra epunctata* Tul., *Hassler 10678* (*US*).—6. *Batesia floribunda* Spruce ex Benth., *Ducke 1699* (*MO*).—7. *Melanoxylon brauna* Schott., *Riedel* and *Lund 2234* (*US*).—8. *Vouacapoua pallidior* Froes, *Froes 21460* (*NY*).—9. *Sclerolobium setiferum* Ducke, *Ducke 343* (*Y*).—10. *Poeppigia procera* Presl., *Hinton 9173* (*US*).—11. *Cenostigma macrophyllum* Tul., *Black, Pires,* and *Lima 54-16450* (*NY*).—12. *Dicymbe froesii* Ducke, *Froes 21372* (*NY*).—13. *Dicymbe duidae* Cowan, *Maguire, Cowan,* and *Wurdack 29666* (*NY*).—14. *Dicymbe altsoni* Sandwith, *Forest Department 5459* (*NY*).

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of exine.

PLATE I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12
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EXINE
COLPUS
OS
EQUATORIAL AXIS
POLAR AXIS
CAPUT
BACULUM
NEXINE
a
b
c
ul
min.
13

Section *Apoxypetala*

Dicymbe uaeparuensis Cowan, *Cardona 1886* (*NY*).

Prolate spheroidal, 49×43 μ, (P/E=1.14). Sexine verrucate with small somewhat irregular mural islands.

Dicymbe duidae Cowan, *Maguire, Cowan*, and *Wurdack 29666* (*NY*)—Plate 1, 13.

Prolate spheroidal, 54×49 μ, (P/E=1.11). Sexine verrucate, mural islands ca. 2× as long as wide.

Diptychandra Tul.—Grains are 3-colporate, united in permanent tetrads with tetrahedral arrangement, ora spherical to rectangular lalongate, sexine reticulate, heterobrochate, simplibaculate, polygonal lumina varying in size from 3 to 5 μ, sexine=2× nexine, no sculptural elements occurring at the point of junction of the grains in the tetrad.

Diptychandra aurantiaca Tul., *Martins 1149* (*P*).

Side a 42* μ, h_a 42* μ, Lumina 4.5 μ.

D. aurantiaca Tul., *Malme 2389*.

Side a 43* μ, h_a 43* μ, Lumina 3.9 μ.

Diptychandra epunctata Tul., *Blanchet 2784* (*NY*).

Side a 40* μ, h_a 45* μ, Lumina 5.0 μ.

D. epunctata, *Hassler 10678* (*US*)—Plate 1, 5.

Side a 43* μ, h_a 46* μ, Lumina 3.0 μ.

Melanoxylon Schott.—Grains are 3-colporate, oblate spheroidal, ora being usually lalongate rectangular, sexine reticulate, lumina varying in size from 2 to 3 μ, heterobrochate.

Melanoxylon brauna Schott, *Campos Portos 10949* (*US*).

Oblate spheroidal, 28×31 μ, (P/E=0.90), Lumina 2.2 μ.

M. brauna, *Mellow Barreto 701*.

Oblate spheroidal, 32×35 μ, (P/E=0.89), Lumina 3.0 μ.

M. brauna, *Riedel* and *Lund 2235* (*US*)—Plate 1, 7.

Oblate spheroidal, 34×36 μ, (P/E=0.97), Lumina 3.1 μ.

M. brauna, *Sellow 945* (*F*).

Oblate speroidal, 34×35 μ, (P/E=0.95), Lumina 3.1 μ.

Recordoxylon Ducke—Grains are 3-colporate, oblate spheroidal, prolate spheroidal, or suboblate, ora rectangular to elliptical lalongate, sexine reticulate, heterobrochate, lumina 2 μ.

Recordoxylon amazonicum Ducke, *Ducke 269* (*F*).

Oblate spheroidal, 33×36 μ, (P/E=0.92).

R. amazonicum, *Ducke 226* (*F*).

Suboblate, 34×40 μ, (P/E=0.87).

R. amazonicum, *Maguire* and *Fanshawe 23050* (*MO*)—Plate 1, 1.

Suboblate, 36×42 μ, (P/E=0.87).

Recordoxylon stenopetalum Ducke, *Ducke 35078* (*US*).

Prolate spheroidal, 34×33 μ, (P/E 1.01).

Sclerolobium Vogel—Grains are 3-colporate, five shape classes, ora varying in shape from rectangular to elliptical or spherical, sexine reticulate to subreticulate, sexine=2–4× nexine, grains occurring in monads and tetrads.

Section *Oriens*

Sclerolobium beaurepairei Harms, *Glaziou 18906*.

Oblate spheroidal, 23×28 μ, (P/E=0.96), reticulate.

Sclerolobium denudatum Vogel, *Hands 119* (*Y*).
Spheroidal, 26×26 μ, (P/E=1.00), reticulate.
Sclerolobium duckei Dwyer, *Barries 48* (*MO*).
Prolate spheroidal, 25×24 μ, (P/E=1.04), reticulate.
Sclerolobium friburgense Harms, *Glaziou 15095*.
Prolate spheroidal, 26×24 μ, (P/E=1.09), reticulate.
Sclerolobium glaziovii Taub., *Oechioni 875* (*P*).
Oblate spheroidal, 24×25 μ, (P/E=0.93), reticulate.
Sclerolobium rugosum Mart. ex Benth., *Lund 390* (*F*).
Prolate spheroidal, 28×22 μ, (P/E=1.05), reticulate.
S. rugosum, *Riedel* and *Wund 2919* (*MO*).
Oblate spheroidal, 23×23 μ, (P/E=0.98), reticulate.
Sclerolobium subbullatum Ducke, *Ducke 12298* (*F*).
Subprolate, 26×22 μ, (P/E=1.18), reticulate.
Sclerolobium urbanianum Harms, *Glaziou 10683*.
Prolate spheroidal, 24×23 μ, (P/E=1.06), reticulate.

Section *Cosymbe*

Sclerolobium aureum (Tul.) Benth., *Pohl 1026* (*W*).
Prolate spheroidal, 22×22 μ, (P/E=1.03), subreticulate.
Sclerolobium macropetalum Ducke, *Ducke 42* (*MO*).
Oblate spheroidal, 27×26 μ, (P/E=0.99), subreticulate.
Sclerolobium micropetalum Ducke, *Ducke 1219* (*US*).
Prolate spheroidal, 20×18 μ, (P/E=1.11), subreticulate.

Section *Sclerolobiastrum*

Sclerolobium melinonii Harms, *Melinon 18* (*F*).
Oblate spheroidal, 23×23 μ, (P/E=0.99), subreticulate.

Section *Eusclerolobium*

Sclerolobium albiflorum Benoist, *Benoist 1074* (*P*).
Prolate spheroidal, 24×22 μ, (P/E=1.08), reticulate. Many of the grains are found to be in tetrads.
Sclerolobium amplifolium Ducke, *Krukoff 8879* (*MO*).
Prolate spheroidal, 22×20 μ, (P/E=1.08), reticulate.
Sclerolobium chrysophyllum Poepp. and Endl., *Poeppig 2666*.
Prolate spheroidal, 25×22 μ, (P/E=1.12), subreticulate.
Sclerolobium densiflorum Benth., *Luschnath 9* (*B*).
Prolate spheroidal, 23×22 μ, (P/E=1.03), subreticulate.
Sclerolobium eriopetalum Ducke, *Ducke 1292*.
Prolate spheroidal, 21×21 μ, (P/E=1.04), subreticulate.
S. eriopetalum, *Ducke 1592* (*F*).
Prolate spheroidal, 25×23 μ, (P/E=1.08), subreticulate.
S. eriopetalum, *Ducke 24296*.
Subprolate, 23×19 μ, (P/E=1.24), subreticulate.
S. eriopetalum, *Ducke 35095* (*MO*).
Prolate spheroidal, 22×21 μ, (P/E=1.08), subreticulate.
Sclerolobium goeldianum Huber, *Ducke 682* (*F*).
Prolate spheroidal, 24×27 μ, (P/E=1.09), subreticulate.
Sclerolobium guianense Benth., *Cuatrecasas 10543*.
Prolate spheroidal, 26×24 μ, (P/E=1.11), subreticulate.

S. guianense, Stahel 89 (Y).
Subprolate, 24×21 μ, (P/E = 1.16), subreticulate.
S. guianense var. *radlkoferi* (Rusby) Dwyer, *Buchtien 1722.*
Subprolate, 25×25 μ, (P/E = 1.20), subreticulate.
Sclerolobium hypoleucum Benth., *Ducke 523 (MO).*
Spheroidal, 25×25 μ, (P/E = 1.00), reticulate.
Sclerolobium macrophyllum Vogel, *St. Hilaire 579 cat B*[1] B₁ *(F)*—Plate 1, 3.
Oblate spheroidal, 28×29 μ, (P/E = 0.97), reticulate.
Sclerolobium melanocarpum Ducke, *Ducke 858 (F).*
Prolate spheroidal, 25×32 μ, (P/E = 1.07), reticulate.
Sclerolobium odoratissimum Spruce ex Benth., *Spruce 3057 (P).*
Prolate spheroidal, 28×26 μ, (P/E = 1.05), subreticulate.
Sclerolobium paniculatum Vogel, *Lutzelburg 1559 (MO).*
Prolate, 27×21 μ, (P/E = 1.34), subreticulate.
Sclerolobium paraense Huber, *Rodrigues 5620.*
Oblate spheroidal, 23×20 μ, (P/E = 0.95), reticulate.
Sclerolobium pilgerianum Harms, *Glaziou 15933 (F).*
Prolate spheroidal, 23×20 μ, (P/E = 1.13), subreticulate.
Sclerolobium rigidum Macbr., *Klug 3239 (F).*
Subprolate, 28×22 μ, (P/E = 1.24), subreticulate.
Sclerolobium setiferum Ducke, *Ducke 343 (Y)*—Plate 1, 9.
Prolate spheroidal, 24×24 μ, (P/E = 1.10), subreticulate.
Sclerolobium striatum Dwyer, *Pessal 62528 (MO).*
Oblate spheroidal, 27×26 μ, (P/E = 0.94), subreticulate.
Sclerolobium tinctorium Benth., *Mexia 6034 (MO).*
Suboblate, 23×27 μ, (P/E = 0.87), reticulate.

Vouacapoua Aubl.—Grains are 3-colporate, shape varying from prolate spheroidal, to oblate spheroidal, ora spherical to rectangular, sexine reticulate, polygonal lumina, heterobrochate, lumina measuring about 1 to 2 μ.

Vouacapoua americana Aubl., *Pires 3104 (NY).*
Oblate spheroidal, 26×26 μ, (P/E = 1.00).
V. americana, B. W. 4256 (MO).
Prolate spheroidal, 30×27 μ, (P/E = 1.10).
V. americana, Melinon s. n. (P).
Prolate spheroidal, 30×26 μ, (P/E = 1.05).
Vouacapoua pallidior Froes, *Froes 21460 (NY)*—Plate 1, 8.
Oblate spheroidal, 26×29 μ, (P/E = 0.90).

Phyllocarpus Riedel—Grains are 3-colporate, shape varying from prolate spheroidal to oblate spheroidal, colpi long and narrow, ora varying from rectangular to elliptical or spherical, sexine finely reticulate, sexine = nexine.

Phyllocarpus riedeleii Tul., *Campos Portos 23623 (US)*—Plate 1, 4.
Oblate spheroidal, 35×37 μ, (P/E = 0.95).
Phyllocarpus septentrionalis Donn. Sm., *Bicknell s. n. (US).*
Oblate spheroidal, 35×36 μ, (P/E = 1.01).
P. septentrionalis, Steyermark and *Allen 76742.*
Prolate spheroidal, 30×30 μ, (P/E = 1.01).

Poeppigia Presl.—Grains are 3-colporate, colpi long and narrow,

subprolate, some constricticolpi, ora circular but not always clearly discernible, sexine very finely reticulate, sexine = nexine.

Poeppigia procera Presl., *Hinton 9173* (*US*)—Plate 1, 10.
Subprolate, 21×17 μ, (P/E = 1.27).

Cynometreae

Aphanocalyx Oliv.—Grains are 3-colporate, shape oblate spheroidal, spherical ora, sexine striate with narrow lirae twisting and anastomosing.

Aphanocalyx cynometroides Oliver, *Zenker 3757* (*US*)—Plate 2, 23.
Oblate spheroidal, 28*×31* μ, (P/E = 0.90).

Copaifera L.—Grains are 3-colporate, shape suboblate, oblate spheroidal, or prolate spheroidal, colpi not meeting at the poles or syncolpate, ora lalongate rectangular to square or spherical, sexine psilate, sexine = nexine or in some 2× nexine, amb triangular or rounded, shape in equatorial view diamond-shaped or elliptical.

Copaifera chodatiana Hassler, *Hassler 8046* (*E*).
Oblate spheroidal, 26×29 μ, (P/E = 0.92).

Copaifera mildbraedii Harms, *Louis 6161* (*US*).
Prolate spheroidal, 26×23 μ, (P/E = 1.13).

Copaifera multijuga Hayne, *Ducke 678* (*NY*).
Suboblate, 23×29 μ, (P/E = 0.80).

C. multijuga, *Ducke 21210* (*NY*).
Suboblate, 22×27 μ, (P/E = 0.79).

Copaifera officinalis L., *Maguire, Kunhardt*, and *Polite 27267* (*NY*).
Suboblate, 21×24 μ, (P/E = 0.88).

Copaifera panamensis (Britton) Standley, *Holt and Gehriger 88* (*NY*).
Suboblate, 20×25 μ, (P/E = 0.83).

Copaifera pubiflora Benth., *Wurdack* and *Bunting 36179* (*NY*)—Plate 2, 21.
Oblate spheroidal, 21×24 μ, (P/E = 0.90).

Copaifera salibounda Heck, *Kennedy 2296* (*US*).
Suboblate, 19×22 μ, (P/E = 0.86).

Copaifera venezuelana Pittier, *Pittier 10991* (*NY*).
Suboblate, 22×26 μ, (P/E = 0.83).

Cryptosepalum Benth.—Grains are 3-colporate, shape prolate to spheroidal, ora spherical to rectangular lalongate, colpi not meeting at the poles, sexine striate with narrow lirae anastomosing and twisting, simplibaculate, rounded amb.

Cryptosepalum fruiticosum Hutch., *Young 204* (*NY*).
Oblate spheroidal, 28×29 μ, (P/E = 0.99).

Cryptosepalum marvaiense Oliv., *Stolz 167a* (*NY*)—Plate 2, 17.
Prolate spheroidal, 29×30 μ, (P/E = 1.03).

Cynometra L.—Grains are 3-colporate, shapes prolate spheroidal, spheroidal, oblate spheroidal, and suboblate, syncolpate or colpi not meeting at the poles, ora spherical to rectangular or elliptical lalongate, sexine psilate or finely striate, sexine = nexine or sexine > nexine.

Cynometra alexandri C. H. Wright, *Eggling 2139* (*NY*).
Prolate spheroidal, 27×24 μ, (P/E = 1.11). The delicately patterned sexine is wider than the nexine.

C. alexandri, *Corbisier 1377* (*MO*).

Prolate spheroidal, $28 \times 23\ \mu$, (P/E = 1.08). Sexine wider than the nexine.

Cynometra aubrevillei Pellegrin, *Aubreville 152 (P)*.

Oblate spheroidal, $25 \times 27\ \mu$, (P/E = 0.96). Striate sexine.

Cynometra aurita Viguier, *19 (P)*.

Prolate spheroidal, $29 \times 28\ \mu$, (P/E = 1.03). Psilate sexine.

Cynometra bauhiniaefolia Benth., *Tessmann 3444 (G)*.

Oblate spheroidal, $20 \times 22\ \mu$, (P/E = 0.94). Psilate sexine, syncolpate.

Cynometra bipetala Pellegr., *Le Testu 7500 (P)*.

Prolate spheroidal, $26 \times 25\ \mu$, (P/E = 1.04). Striate sexine.

Cynometra dacremontii Vibrun, *Dacremont 352 (MO)*.

Oblate spheroidal, $23 \times 25\ \mu$, (P/E = 0.94). Striate sexine.

Cynometra fissicuspis Pittier, *Niceforo 16 (US)*—Plate 2, 15.

Prolate spheroidal, $23 \times 22\ \mu$, (P/E = 1.06). Psilate sexine.

Cynometra hankei Harms, *Louis 10006 (MO)*.

Prolate spheroidal, $24 \times 22\ \mu$, (P/E = 1.10). Striate sexine.

Cynometra hostmanniana Tul., *Versleeg 552 (US)*.

Spheroidal, $23^* \times 23^*\ \mu$, (P/E = 1.00).

Cynometra leptantha Harms, *Zenker 3370 (MO)*.

Prolate spheroidal, $29 \times 29\ \mu$, (P/E = 1.01). Striate sexine.

Cynometra pedicellata De Wild., *Louis 13945 (MO)*.

Oblate spheroidal, $26 \times 27\ \mu$, (P/E = 0.97). Striate sexine.

Cynometra sessiliflora Harms var. *laurentii* (De Wild.) Lebrun., *J. Louis 166 (MO)*.

No measurements were possible because of the poor specimen. Striate sexine.

Cynometra spruceana Benth., *Kuhlmann 17655 (U)*.

Suboblate, $26 \times 31\ \mu$, (P/E = 0.84). Sexine somewhat patterned, sexine thicker than nexine.

C. spruceana, Ducke 35415 (Gen.).

Prolate spheroidal, $23 \times 31\ \mu$, (P/E = 1.03). Faintly striate.

Detarium Juss.—Grains are 3-colporate, shape prolate spheroidal,

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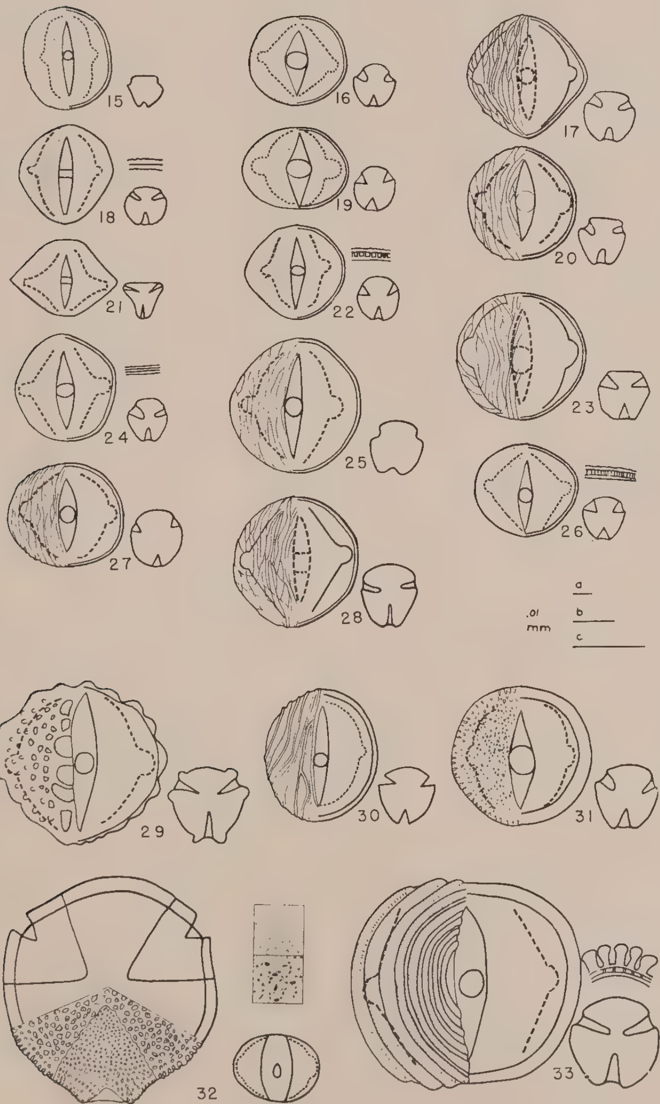
EXPLANATION OF PLATE II

PLATE 2.—Palynograms of the Cynometreae.—15. *Cynometra fissicuspis* Pittier, *Niceforo 16 (US)*.—16. *Gossweilerodendron balsamiferum* (Verm.) Harms, *Louis 2813 (MO)*.—17. *Cryptosepalum maraviense* Oliv., *Stolz 167a (NY)*.—18. *Hardwickia binata* Roxb., *Wright 87a (NY)*.—19. *Kingiodendron* sp., *Waterhouse 172*.—20. *Scorodophloeus zenkeri* Harms, *Zenker 2245 (P)*.—21. *Copaifera pubiflora* Benth., *Wurdack* and *Bunting 36179 (NY)*.—22. *Oxystigma stapfiana* A. Chev., *Coopr. 256 (NY)*.—23. *Aphanocalyx cynometroides* Oliv., *Zenker 3757 (US)*.—24. *Prioria elephantipes*, *Harris 11814 (US)*.—25. *Monopetalanthus pectinatus* Chev., *Le Testu 6069*.—26. *Guibourtia arnoldiana* (De Wild. et Th. Dur.) Leonard, *Flamagni 10118 (NY)*.—27. *Talbotiella eketensis* Bak., *Talbot 3625 (NY)*.—28. *Plagiosiphon discifer* Harms, *Staudt 145 (P)*.—29. *Maniltoa grandiflora* Scheff., *Beccari 178 (US)*.—30. *Hymenostegia afzelii* (Oliv.) Harms, *Vique 1042 (US)*.—31. *Detarium senegalense* Gmel., *Broadway 6917 (US)*.—32. *Stahlia maritima* Bello, *Urban 3876 (F)*.—33. *Neochevalierodendron stephanii* (A. Chev.) Leonard, *Le testu 5754 (P)*.

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of the exine.

PLATE II



spherical ora, very narrow and irregular muri forming a delicate indefinite reticulum, bacula long and densely packed, sexine = 4 × nexine.

Detarium senegalense Gmel., *Broadway 6917* (*US*)—Plate 2, 31.
Prolate spheroidal, 33×32 μ, (P/E = 1.02).

Gilletiodendron Harms—Grains are 3-colporate, shape oblate spheroidal, or rectangular, spherical or elliptical, rounded amb, striate sexine.

Gilletiodendron mildbraedii (Harms) Vermoesen, *Jean Louis 57511* (*MO*).
Oblate spheroidal, 25×27 μ, (P/E = 0.92).
G. mildbraedii, *Jean Louis 15693* (*NY*).
Oblate spheroidal, 26×29 μ, (P/E = 0.88).

Gossweilerodendron Harms—Grains are 3-colporate, shape oblate spheroidal, ora rectangular, spherical or elliptical, psilate sexine, rounded amb.

Gossweilerodendron balsamiferum (Verm.) Harms, *Louis 2813* (*MO*)—Plate 2, 16.
Oblate spheroidal, 22×24 μ, (P/E = 0.92).

Guibourtia Benn.—Grains are 3-colporate, suboblate shape, sexine psilate, ora shape from spherical to elliptical or rectangular.

Guibourtia arnoldiana (De Wild. et Th. Dur.) Leonard, *Flamagni 10118* (*NY*)—Plate 2, 26.
Suboblate, 23×26 μ, (P/E = 0.87).
Guibourtia conjugata (Bolle) Leonard, *Rogers 5832* (*US*).
Suboblate, 25×30 μ, (P/E = 0.87).

Hardwickia Roxb.—Grains are 3-colporate, shape prolate spheroidal, spherical to elliptical ora, psilate with a faintly patterned surface, amb somewhat rounded.

Hardwickia binata Roxb., *Wright 87a* (*NY*)—Plate 2, 18.
Prolate spheroidal, 22×22 μ, (P/E = 1.04).

Hymenostegia (Benth.) Harms sensu. ampl. J. Leonard—Grains are 3-colporate, shape oblate spheroidal, ora spherical or rectangular and elliptical either lolongate or lalongate, striate with very coarse lirae fragmented or unfragmented or fine lirae, rounded amb.

Hymenostegia afzelii (Oliv.) Harms, *Vique 1042* (*US*)—Plate 2, 30.
Oblate spheroidal, 31×32 μ, (P/E = 0.98), Unfragmented lirae.
Hymenostegia aubrevillei Pellegr., *Aubreville 1805* (*P*).
Spheroidal, 34×34 μ, (P/E = 1.00), Fragmented lirae.
Hymenostegia floribunda (Benth.) Harms, *Morel 43* (*P*).
Not sufficient to measure, unfragmented lirae.
Hymenostegia talbotii Baker, *Talbot 3141* (*MO*).
Prolate spheroidal, 38×37 μ, (P/E = 1.02). Extremely fine lirae.
Hymenostegia laxiflora Harms, *Gossweiler 6742* (*MO*).
Prolate spheroidal, 37×36 μ, (P/E = 1.05). Somewhat fragmented lirae.

Kingiodendron Harms—Grains are 3-colporate, shape prolate spheroidal, or spherical to elliptical lolongate or square, psilate with a delicate pattern, sexine = nexine, rounded amb.

Kingiodendron sp., *Waterhouse 172*—Plate 2, 19.
Prolate spheroidal, 25×24 μ, (P/E = 1.05).

Maniltoa Scheffer—Grains are 3-colporate, shape oblate spheroidal to prolate spheroidal, spherical to rectangular or elliptical lalongate ora,

verrucate, amb triangular with slightly convex sides, verrucae not supported by bacula, some crassimarginate.

Maniltoa floribunda A. C. Smith, *A. C. Smith 4627* (*US*).

Prolate spheroidal, 32*×28* μ, (P/E=1.12). Verrucae very small and evenly distributed over the grain.

Maniltoa gemmipara Scheff. ex Becker, *cult. Hort. Bot. 406*.

Oblate spheroidal, 32*×36* μ, (P/E=0.89). Verrucae evenly distributed over the grain surface.

Maniltoa grandiflora Scheff., *Beccari 178* (*US*)—Plate 2, 29.

Oblate spheroidal, 36×39 μ, (P/E=0.98). Verrucate, crassimarginate.

Maniltoa megalocephala Harms, *Hoagland 3883* (*US*).

Oblate spheroidal, 42×44 μ, (P/E=0.96). Verrucae uniformly distributed over the grain surface.

Monopetalanthus Harms—Grains are 3-colporate, shape oblate spheroidal, spherical ora, striate sexine, rounded amb with somewhat truncate apices.

Monopetalanthus pectinatus Chev., *Le Testu 6069*—Plate 2, 25.

Oblate spheroidal, 29×31 μ, (P/E=0.92).

Neochevalierodendron Leonard—Grains are 3-colporate, shape oblate spheroidal, very narrow colpi with spherical ora, striate sexine, parallel arrangement of broad lirae with no anastomosing, multibaculate, rounded amb.

Neochevalierodendron stephanii (A. Chev.) Leonard, *Le Testu 5754* (*P*).

Oblate spheroidal, 48×53 μ, (P/E=0.92).

Oxystigma Harms—Grains are 3-colporate, shape oblate spheroidal, rectangular to elliptical ora, psilate sexine, sexine=nexine, triangular amb with slightly convex sides.

Oxystigma stapfiana A. Chev., *Coopr. 256* (*NY*)—Plate 2, 22.

Oblate spheroidal, 22×24 μ, (P/E=0.93).

Plagiosiphon Harms—Grains are 3-colporate, shape spheroidal, ora spherical to rectangular lalongate, sexine very sparsely striate with fine lirae.

Plagiosiphon discifer Harms, *Staudt 145*—Plate 2, 28.

Spheroidal, 30*×30* μ, (P/E=1.00).

Prioria Gris.—Grains are 3-colporate, prolate spheroidal or spheroidal, ora spherical to rectangular lalongate, sexine psilate to a condition in which the surface is faintly patterned, sexine=nexine, triangular amb with slightly convex sides.

Prioria copaifera Gris., *C. L. Smith 50* (*US*).

Spheroidal, 22×22 μ, (P/E=1.00).

Prioria elephantipes (nomen nudum), *Harris 11814*—Plate 2, 24.

Prolate spheroidal, 25×23 μ, (P/E=1.09).

Pseudocopaiva Britton and Wilson—Grains are 3-colporate, subolate, ora spherical to rectangular, sexine psilate, sexine=nexine, triangular amb.

Pseudocopaiva hymeniaefolia (Moric) Britton et Wilson, *Wright 189* (*MO*).

Suboblate, 24×28 μ, (P/E=0.86).

Pterogyne Tul.—Grains are 3-colporate, subprolate, colpi long and narrow, spherical to rectangular ora, psilate sexine, sexine = nexine.

Pterogyne nitens Tul., *Harris 11513* (*NY*).

Subprolate, $18 \times 14\ \mu$, (P/E = 1.30).

Scorodophloeus Harms—Grains are 3-colporate, shape oblate spheroidal, ora spherical, sexine very sparsely striate, rounded amb.

Scorodophloeus zenkeri Harms, *Zenker 2245* (*P*)—Plate 2, 20.

Oblate spheroidal, $25 \times 25\ \mu$, (P/E = 0.99).

Stahlia Bello—Grains are 3-colporate, shape suboblate, wide colpi marked by the presence of long narrow clavae forming somewhat of a reticulum, lolongate elliptical ora, reticulate sculpturing, simplibaculate, polygonal lumina, heterobrochate, lumina ca. $3\ \mu$, amb somewhat fossapertuate.

Stahlia maritima Bello, *Urban 3876* (*F*)—Plate 2, 32.

Suboblate, $39 \times 47\ \mu$, (P/E = 0.82).

Talbotiella Bak.—Grains are 3-colporate, shape oblate spheroidal, ora rectangular to spherical, sexine very delicately striate, sexine = nexine, rounded amb.

Talbotiella eketensis Bak., *Talbot 3625* (*NY*)—Plate 2, 27.

Oblate spheroidal, $27 \times 28\ \mu$, (P/E = 0.96).

Amherstieae

Afzelia Smith—Grains are 3-colporate or 6-colporate with 3 pseudocolpi, brevicolpi, shape spheroidal to oblate spheroidal, spherical to lolongate ora, sexine reticulate, heterobrochate, polygonal lumina to foveolae, muri supported by bacula and bacularia, smooth contours of muri about the lumina, muri size varying from 2 to $5\ \mu$, lumina size varying from 7 to $15\ \mu$, crassisexinous, (sexine = $5\times$ nexine) fossapertuate.

Afzelia africana Smith ex Pers., *Brown 2160* (*US*)—Plate 3, 35.

Spheroidal, $48 \times 48\ \mu$, (P/E = 1.00), 6-colporate with 3 pseudocolpi.

Afzelia bipindensis Harms, *Ross 25* (*NY*).

Oblate spheroidal, $57 \times 63\ \mu$, (P/E = 0.92), 3-colporate, some of the grains occurring in tetrads.

Amherstia Wall—Grains are 3-colporate, shape prolate spheroidal to subprolate, colpi narrow, ora circular often with irregular margins, sexine striate, fragmentimurate, dupli- and multi-baculate, some tending to be verrucate, crassisexinous, (sexine = $5\times$ nexine), muri supported by distinct bacula, triangular amb.

Amherstia nobilis Wall, *Broadway 5269* (*F*)—Plate 5, 56.

Prolate spheroidal, $55 \times 52\ \mu$, (P/E = 1.06).

A. nobilis, da Silva 48457 (*NY*).

Subprolate, $53 \times 41\ \mu$, (P/E = 1.32).

Baikiaea Benth.—Grains are 3-colporate, shape suboblate, brevicolpate, ora rectangular lalongate, reticulate sexine, large lumina measuring ca. $7.7\ \mu$, angustimurate, heterbrochate, polygonal lumina, very small lumina at the poles and colpi margins measuring ca. $2\ \mu$, grains in equatorial view diamond-shaped, amb triangular.

Baikiaea plurijuga Harms, *Prain 9445* (*MO*)—Plate 3, 40.

Suboblate, $46 \times 56\ \mu$, (P/E = 0.87).

Berlinia Soland ex Hook.—Grains are 3-colporate, shape prolate, prolate spheroidal, and oblate spheroidal, ora spherical to elliptical,

narrow colpi, sexine striate, simplibaculate, crassisexinous, (sexine = 4× nexine), rounded amb.

Berlinia angolensis Welw. ex Benth., *Welwitsch 569* (*P*).
Prolate, 55×39 μ, (P/E = 1.42).
Berlinia auriculata Benth., *Kennedy 800* (*NY*).
Oblate spheroidal, 52×54 μ, (P/E = 0.96).
Berlinia grandiflora (Vahl.) Hutch. and Dalz., *Jean Louis 860* (*NY*)—Plate 5, 57.
Prolate spheroidal, 60×57 μ, (P/E = 1.07).

Brachystegia Benth.—Grains are 3-colporate, shape oblate spheroidal, brevicolpate, ora somewhat sperhical, sexine at apocolpia clavate with some fusion of the capita to form muri, sexine at the mesocolpia coarsely reticulate with lumina size ca. 12 μ, wide muri measuring 3.0 μ, lumina polygonal to foveolate, smooth contours of muri about the lumina, fossapertuate.

Brachystegia taxifolia Harms, *Brass 17358* (*NY*)—Plate 3, 36.
Oblate spheroidal, 41×45 μ, (P/E = 0.91).

Brownea Jacq.—Grains are 3-colporate, shape oblate sperhoidal, ora varying from spherical to elliptical or rectangular lalongate, prolate spheroidal, subprolate, and prolate, sexine varying interspecifically from verrucate to reticulate, the reticulate pattern varying from one in which the reticulation diminishes in coarseness towards the colpi and polar regions to one in which the reticulation is uniform over the surface.

Brownea disepala Little, *Haught 3131* (*NY*)—Plate 4, 46.
Oblate spheroidal, 46×49 μ, (P/E = 0.94), verrucate sexine.
Brownea grandiceps Jacq., *Wurdack* and *Monachino 41015* (*NY*).
Subprolate, 47×40 μ, (P/E = 1.21).
Sexine uniformly reticulate over the grain surface.
Brown latifolia Jacq., *Wurdack* and *Monachino 39575* (*NY*)—Plate 3, 41.
Prolate spheroidal, 45*×42* μ, (P/E = 1.08).
B. latifolia, *Llewelyn* and *Williams 12565* (*F*).
Prolate spheroidal, 43×40 μ, (P/E = 1.07), sexine uniformly reticulate.
Brownea leucantha Jacq., *Bernardi 1022* (*NY*).
Prolate, 58×43 μ, (P/E = 1.38), sexine reticulate with diminishing lumina size towards the polar and colpi regions.
Brownea longipedicellata Hub., *Archer 7555* (*NY*).
Subprolate, 44*×38* μ, (P/E = 1.17), sexine uniformly reticulate.
Brownea macbrideana Staudt. *Klug 2035*—Plate 3, 39.
Subprolate, 70*×53* μ, (P/E = 1.31), sexine reticulate with diminishing lumina size in the polar and colpi regions.
Brownea macrophylla Linden, *Toro 107* (*NY*).
Subprolate, 59*×50* μ, (P/E = 1.20), sexine the same as *B. macbrideana*.
Brownea rosa de Monte Berg., *Broadway 5569* (*MO*).
Subprolate, 49*×39* μ, (P/E = 1.25), reticulate, somewhat coarser in the mesocolpi than elsewhere.
Brownea similis Cowan, *Maguire* and *Polite 28968 A* (*NY*).
Prolate spheroidal, 45×39 μ, (P/E = 1.14), sexine uniformly reticulate.

Brownea sp., *Standley 30195* (*US*).
Prolate spheroidal, 56×51 μ, (P/E=1.06), sexine reticulate with a slight diminishing of reticulum towards the apocolpia.

Crudia Schreb.—Grains are 3-colporate, shape showing great variation and representing six shape classes, syncolpate to colpi not meeting at the poles, ora not very prominent, varying from spherical to elliptical lolongate, colpi long, narrow, and psilate, sexine striate with regular lirae in parallel arrangement running the entire length of the grain.

Crudia aequalis Ducke, *Ducke 740* (*NY*).
Oblate spheroidal, 37×39 μ, (P/E=0.96).
Crudia amazonica Spruce ex Benth., *Ducke 24287* (*US*).
Subprolate, 39×33 μ, (P/E=1.18), some grains syncolpate.
Crudia antillana Urb., *Ekman 3569* (*NY*).
Prolate spheroidal, 31×28 μ, (P/E=1.10).
Crudia aromatica (Aubl.) Willd., *McGuire 24903* (*US*).
Prolate spheroidal, 44×42 μ, (P/E=1.04).
Crudia bantamensis (Hassk.) Benth., *Toroes 3863* (*US*).
Oblate spheroidal, 31*×34* μ, (P/E=0.92).
Crudia blancoi Merrill, *Ahern 3136* (*US*).
Subprolate, 29×23 μ, (P/E=1.25).
Crudia bracteata Benth., *Ducke 1604* (*US*)—Plate 5, 60.
Oblate spheroidal, 32×33 μ, (P/E=0.99).
Crudia falcata Klotzsch, *Schomburgk 841* (*NY*).
Subprolate, 39×30 μ, (P/E=1.30).
Crudia glaberrima (Steud.) Macbr., *Gongyrpp 3532* (*US*).
Subprolate, 35×28 μ, (P/E=1.30).
Crudia obliqua Griseb., *Hort. 2239*.
Subprolate, 41×32 μ, (P/E=1.30).
Crudia oblonga Benth., *Bot. Gard. Trinidad 3082* (*US*).
Subprolate, 37×31 μ, (P/E=1.19).
Crudia paraensis (nomen nudum), *Huber 9398*.
Prolate, 45×33 μ, (P/E=1.46).
Crudia parivoa D. C. Prod., *Ducke 606* (*US*)
Subprolate, 35×30 μ, (P/E=1.15).
Crudia pubescens Spruce ex Benth., *Gines 5158* (*US*).
Prolate spheroidal, 29×27 μ, (P/E=1.07).
Crudia reticulata Merrill, *Elmer 20708* (*NY*).
Prolate spheroidal, 32×31 μ, (P/E=1.02), some grains are syncolpate.
Crudia spicata (Aubl.) Willd., *Huber 7895* (*US*).
Prolate spheroidal, 32×31 μ, (P/E=1.03).
Crudia tomentosa (Aubl.) Macbr., *Froes 1493* (*US*).
Prolate, 34×26 μ, (P/E=1.34).
Crudia zenkeri Harms, *Zenker 542* (*NY*)—Plate 5, 51.
Oblate, 16×22 μ, (P/E=0.73). The pollen of this species in contrast to the pollen of all of the other species studied, is a much smaller grain, is oblate in shape, and bears a psilate sexine.

Daniella J. J. Benn.—Grains are 3-colporate, suboblate, very wide colpi with spherical to elliptical or rectangular lalongate ora, psilate sexine, bacula not present, sexine=nexine.

Daniella thurifera J. J. Benn., *Benoist Coopr. 95* (*F*).

PLATE III

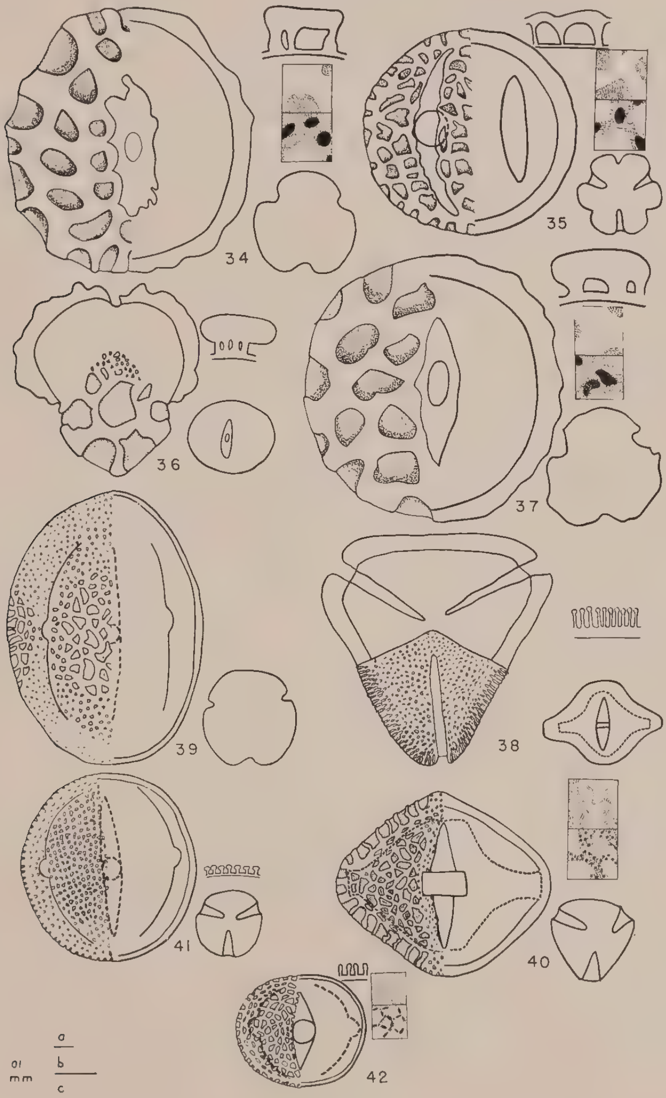


PLATE 3.—Palynograms of the reticulate pollen of the Amherstieae.—34. *Intsia bijuga* (Colebr.) O. K., *R. S. Williams 2738* (*NY*).—35. *Afzelia africana* Smith ex Pers., *Brown 2160* (*US*).—36. *Brachystegia taxifolia* Harms, *Brass 17358* (*NY*).—37. *Pahudia rhomboidea* (Blanco) Prain, *Fenix 1148* (*US*).—38. *Sindora wallichii* Graham ex Benth., *Ridley s. n.* (*F*).—39. *Brownea macbrideana* Staudt, *Klug 2035*.—40. *Baikiaea plurijuga* Harms, *Prain 9445* (*MO*).—41. *Brownea latifolia* Jacq., *Wurdack* and *Monachino*.—42. *Tachigalia pubiflora* Benth., *Anderson 752* (*US*).

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of exine.

Suboblate, 32×39 μ, (P/E=0.82).

Daniella sp., *Ghesquiere 2686* (*P*)—Plate 5, 55.

Suboblate, 38*×45* μ, (P/E=0.84).

Didelotia Baill.—Grains are 3-colporate, shape prolate, very narrow colpi, spherical to elliptical lolongate ora, sexine striate, very regular lirae arranged in parallel rows, sexine=4× nexine, crassisexinous, triangular amb with convex sides.

Didelotia africana Baill., *Du Bellay 235* (*P*)—Plate 5, 59.

Prolate, 44×30 μ, (P/E=1.47).

Elizabetha Schomb.—Grains are 3-colporate, shape prolate spheroidal to subprolate, spherical ora, narrow psilate colpi, sexine verrucate with granulate interspaces, verrucae round or polygonal, supported by bacula in some grains, crassisexinous, amb triangular with slightly convex sides.

Elizabetha duckei Huber, *Froes 28100*—Plate 4, 43.

Oblate spheroidal, 64×68 μ, (P/E=0.94), verrucae 12.2 μ. The verrucae of this grain are very sparsely distributed.

Elizabetha paraensis Ducke, *Siguera 34958*.

Subprolate, 59×50 μ, (P/E=1.18), verrucae 9.1 μ.

E. paraensis, *Ducke 591* (*US*)—Plate 4, 44.

Prolate spheroidal, 55×52 μ, (P/E=1.05), verrucae 8.7 μ.

Elizabetha princeps Schomb. ex Benth., *Wurdack* and *Bunting 36736* (*NY*).

Prolate spheroidal, 59×57 μ, (P/E=1.05).

Eperua Aubl.—Grains are 3-colporate with brevicolpi to 3-apertuate, shape varies from suboblate to oblate, sexine varying from retipilate, clavate baculate, ornate to verrucate, amb variable from a triangular one to one in which the apices are greatly extended into long arms and terminating in apertures not surrounded by colpi.

Eperua bijuga Mart. ex Benth., *Ducke 158* (*MO*).

Oblate, 35*×70* μ, (P/E=0.51).

Sexine clavate baculate, 3-colporate, brevicolpate.

Eperua campestris Ducke, *Ducke 23291* (*US*)—Plate 6, 66.

Suboblate, 41*×50* μ, (P/E=0.81), sexine retipilate, lumina size about 5 μ, lumina approach the homobrochate condition in regularity of size.

Eperua falcata Aubl., *B. W. 4791* (*MO*)—Plate 6, 63.

Oblate, 63*×113* μ, (P/E=0.56), sexine ornate, crassisexinous, increase in height of sexine at colpi margins, lumina 18 μ, 3-colporate with brevicolpi.

Eperua grandiflora (Aubl.) Benth., *Steyermark 75537* (*NY*)—Plate 6, 65.

Oblate, 46*×73* μ, (P/E=0.64), sexine clavate baculate, 3-apertuate.

Eperua leucantha Benth., *Froes 21104* (*NY*).

Oblate, 53*×95* μ, (P/E=0.56),verrucate sexine, verrucae supported by regular bacula.

Eperua oleifera Ducke, *Ducke 23290* (*P*).

Suboblate, 47*×54* μ, (P/E=0.88), pollen similar to *E. campestris* Ducke.

Eperua purpurea Benth., *Schultes*, *Baker*, and *Cabrera 17955* (*NY*).

PLATE IV

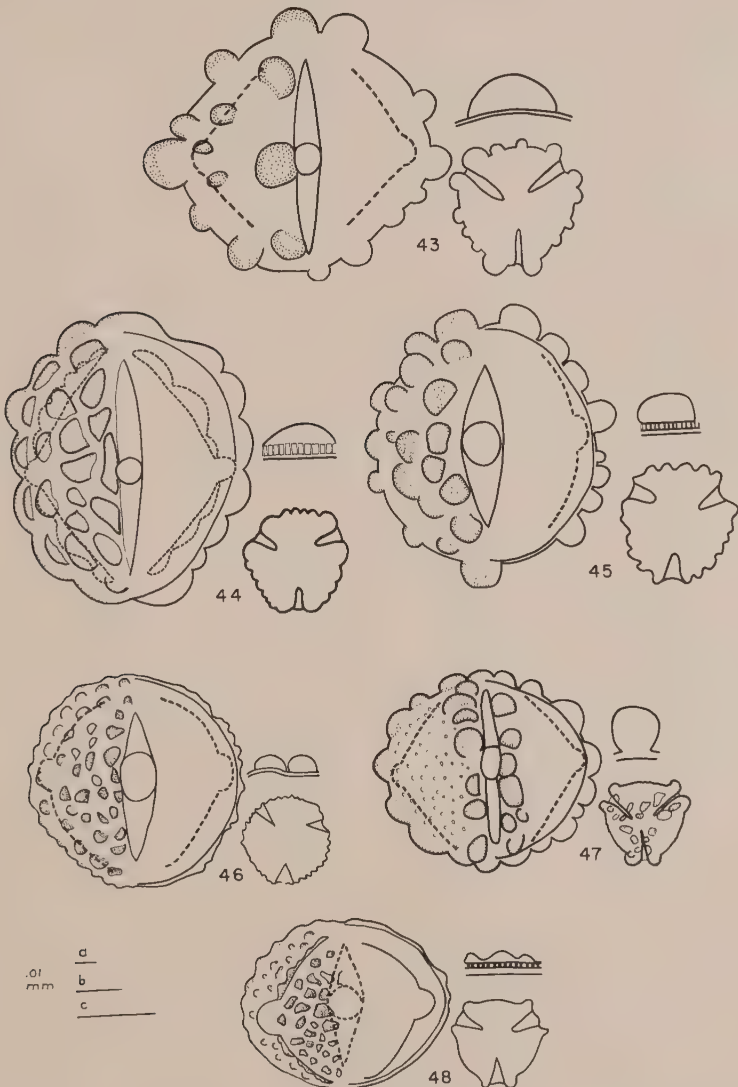


PLATE 4.—Palynograms of the verrucate pollen of the Amherstieae.—43. *Elizabetha duckei* Huber, *Froes 28100*.—44. *Elizabetha paraensis* Ducke, *Ducke 591* (*US*).—45. *Palovea riparia* Pulle, *Cowan 38814* (*NY*).—46. *Brownea disepala* Little, *Haught 3131* (*NY*).—47. *Palovea brasiliensis* Ducke, *Ducke 10882* (*NY*).—48. *Peltogyne densiflora* Spr. ex Benth., *Ducke 23275* (*NY*).

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of the exine.

It was impossible to obtain accurate measurements of the grains because of the poor material. Otherwise these grains are like those of *E. oleifera* and *E. campestris*.

Eperua rubiginosa Miq., *B. W. 725* (*MO*)—Plate 6, 64.

Oblate, 63*×96* μ, (P/E=0.65), sexine verrucate with large baculate interspaces.

Eperua schomburgkiana Benth., *Sandwith 142* (*P*).

Oblate, 33*×65* μ, (P/E=0.51), sexine clavate baculate, brevicolpate though in some the colpi are not so evident.

Heterostemon Desf.—Grains are 3-colporate, distinctly spherical ora, shape subprolate to prolate spheroidal, narrow colpi, sexine very finely striate, circular amb.

Heterostemon ellipticus Mart. ex Benth., *Ducke 41* (*F*)—Plate 5, 62.

Prolate spheroidal, 64*×62* μ, (P/E=1.03), frequently grains with only two colpi arranged perpendicular to each other were noted in this preparation.

Heterostemon mimosoides Desf., *Ducke 768* (*US*).

Subprolate, 58×50 μ, (P/E=1.16).

Hylodendron Taub.—Grains are 3-colporate, shape suboblate, spherical to elliptical lalongate ora, psilate sexine, sexine=nexine, triangular amb with concave to straight sides, shape of grain in equatorial view is diamond-shaped.

Hylodendron gabunense Taub., *Le Testu 7605* (*P*).

Suboblate, 17×20 μ, (P/E=0.86).

H. gabunense, *Zenker 3784* (*US*)—Plate 5, 50.

Suboblate, 16×19 μ, (P/E=0.83).

Hymenaea L.—Grains are 3-colporate, shape oblate spheroidal, prolate spheroidal, and subprolate, ora very distinct varying in size from spherical to elliptical lolongate, colpi long and narrow, sexine psilate to finely reticulate, sexine=nexine, rounded amb, some crassimarginate.

Hymenaea oblongifolia Hub., *Krukoff 6323* (*NY*).

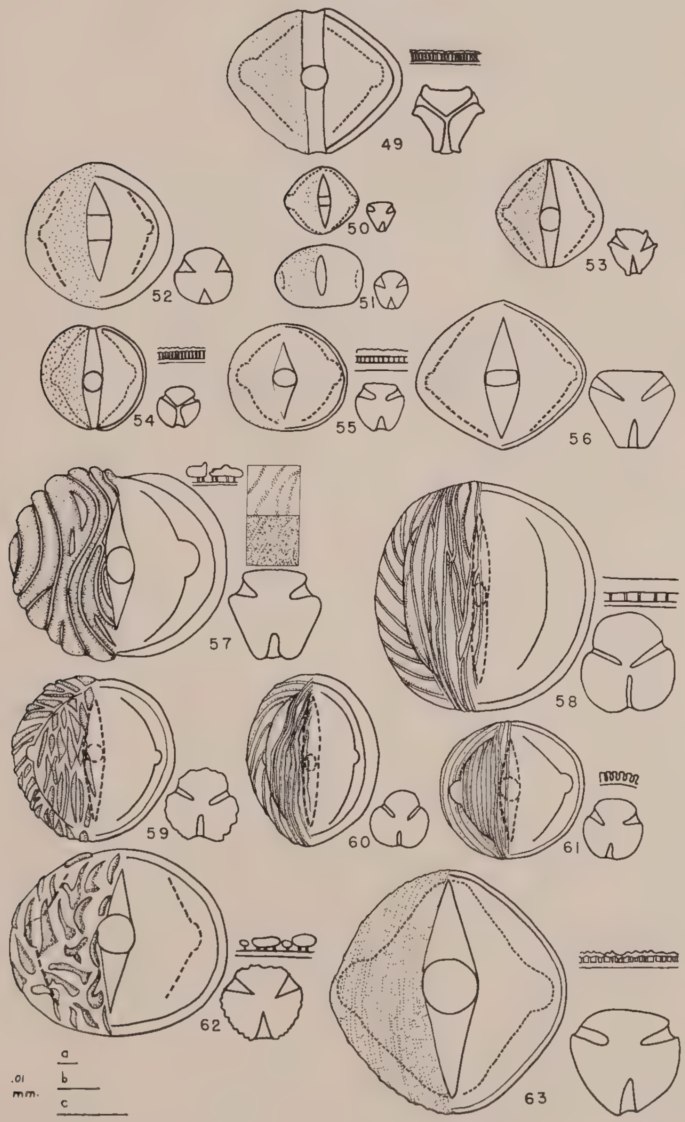
Prolate spheroidal, 28×26 μ, (P/E=1.05), sexine psilate and thickened at the colpi margins, crassimarginate, syncolpate or colpi ending near the poles.

EXPLANATION OF PLATE V

PLATE 5.—Palynograms of the striate and psilate pollen of the Amherstieae. 49. *Tessmannia yangambiensis* Louis ex J. Leonard, *Louis 10111* (*US*).—50. *Hylodendron gabunense* Taub., *Zenker 3784* (*US*).—51. *Crudia zenkeri* Harms, *Zenker 542* (*NY*).—52. *Peltogyne floribunda* (H. B. K.) Benth., *Ducke 331* (*NY*).—53. *Hymenaea oblongifolia* Hub., *Krukoff 6323* (*NY*).—54. *Trachylobium verrucosum* (Gaertn.) Oliv., *Imperial Forestry Instit. Coll. 398*.—55. *Peltogyne pubescens* Benth., *Schomburgk 791* (*NY*).—56. *Daniella* sp., *Ghesquiere 2686* (*P*).—57. *Amherstia nobilis* Wall, *Broadway 5269* (F).—58. *Berlinia grandiflora* (Vahl.) Hutch. and Dalz., *Jean Louis 860* (*NY*).—59. *Macrolobium rubrum* Cowan, *Maguire, Wurdack*, and *Keith 41810* (*NY*).—60. *Didelotia africana* Baill., *Du Bellay 235* (*P*).—61. *Crudia bracteata* Benth., *Ducke 1604* (*US*).—62. *Lysidice rhodostegia* Hance, *E. Anderson 120* (*US*).—63. *Heterostemon ellipticus* Mart. ex Benth., *Ducke 41* (*F*).

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of exine.

PLATE V



Hymenaea parvifolia Huber, *Froes 237* (*NY*).
Oblate spheroidal, 42×43 μ, (P/E=0.98), sexine finely reticulate, colpi not meeting at the poles, not crassimarginate.
Hymenaea stilbocarpa Hayne, *Dahlgren 887* (*US*).
Subprolate, 50×44 μ, (P/E=1.16), finely reticulate sexine, colpi not meeting at the poles, not crassimarginate.

Intsia Thou.—Grains are 3-colporate, shape prolate spheroidal, spherical to elliptical lolongate ora, brevicolpi, coarsely reticulate, lumina polygonal to foveolate, lumina surrounded by smooth contours of the muri, broad muri supported by bacula or bacularia, lumina 11 to 18 μ, muri measure ca. 4 μ, crassisexinous, (sexine=7–9× nexine), fossapertuate.
Intsia bijuga (Colebr.) O. K., *Ramos 17428* (*MO*).
Prolate spheroidal, 68*×65* μ, (P/E=1.06), lumina 11.5 μ, muri 3.7 μ.
I. bijuga, *R. S. Williams 2738* (*NY*)—Plate 3, 34.
Prolate spheroidal, 63×57 μ, (P/E=1.11), lumina 11 μ, muri 3.9 μ.

Lysidice Hance—Grains are 3-colporate, shape oblate spheroidal, spherical ora, narrow psilate colpi, sexine rugulate, prominent bacula, duplibaculate, sexine=3× nexine, rounded amb.
Lysidice rhodostegia Hance, *E. Anderson 120* (*US*)—Plate 5, 61.
Oblate spheroidal, 46×49 μ, (P/E=0.94).

Macrolobium Schreb.—Grains are 3-colporate, shape prolate, subprolate, and prolate spheroidal, ora mostly spherical, narrow psilate colpi, sexine striate with lirae often fragmented and curved, sexine=3–4× nexine, rounded amb.
Macrolobium acaciaefolia (Benth.) Benth., *de la Cruz 1925* (*MO*).
Subprolate, 42×34 μ, (P/E=1.24).
Macrolobium angustifolium (Benth.) Cowan, *de la Cruz 1799* (*NY*).
Prolate, 44×32 μ, (P/E=1.38).
Macrolobium molle (Benth.) Cowan, *L. Williams 15976* (*NY*).
Prolate, 42×30 μ, (P/E=1.41).
Macrolobium rubrum Cowan, *Maguire*, *Wurdack*, and *Keith 41810* (*NY*)—Plate 5, 58.
Prolate spheroidal, 41×39 μ, (P/E=1.05).

Oddoniodendron De Wild.—Grains are 3-colporate, shape prolate spheroidal, ora mostly spherical some lalongate, narrow colpi, sexine striate, sexine=nexine, amb triangular with slightly convex sides.
Oddoniodendron gilletii De Wild., *Le Testu 7493* (*P*).
Prolate spheroidal, 34×34 μ, (P/E=1.02).

Pahudia Miq.—Grains are 3-colporate, shape oblate spheroidal, spherical to lolongate ora, psilate brevicolpi, sexine coarsely reticulate, foveolate or polygonal lumina, smooth contours about the lumina, simplibaculate and simplibaculariate, lumina 6.8 to 14.4 μ, muri 2.3 to 4.4 μ, crassisexinous, (sexine=5× nexine), fossapertuate.
Pahudia cochinchinensis Pierre, *Chevalier 31315* (*P*).
Oblate spheroidal, 59×63 μ, (P/E=0.95), lumina 6.8 μ, muri 3.2 μ.
Pahudia rhomboidea (Blanco) Prain, *Aherns 3263* (*US*).
Oblate spheroidal, 58×64 μ, (P/E=0.91), lumina 13.9 μ, muri 2.3 μ.
P. rhomboidea, *Fenix 1148* (*US*)—Plate 3, 37.
Oblate spheroidal, 63×66 μ, (P/E=0.95), lumina 13.7 μ, muri 4.4 μ.
Pahudia martabanica Prain, *Rauzada s. n.* (*MO*).

PLATE VI

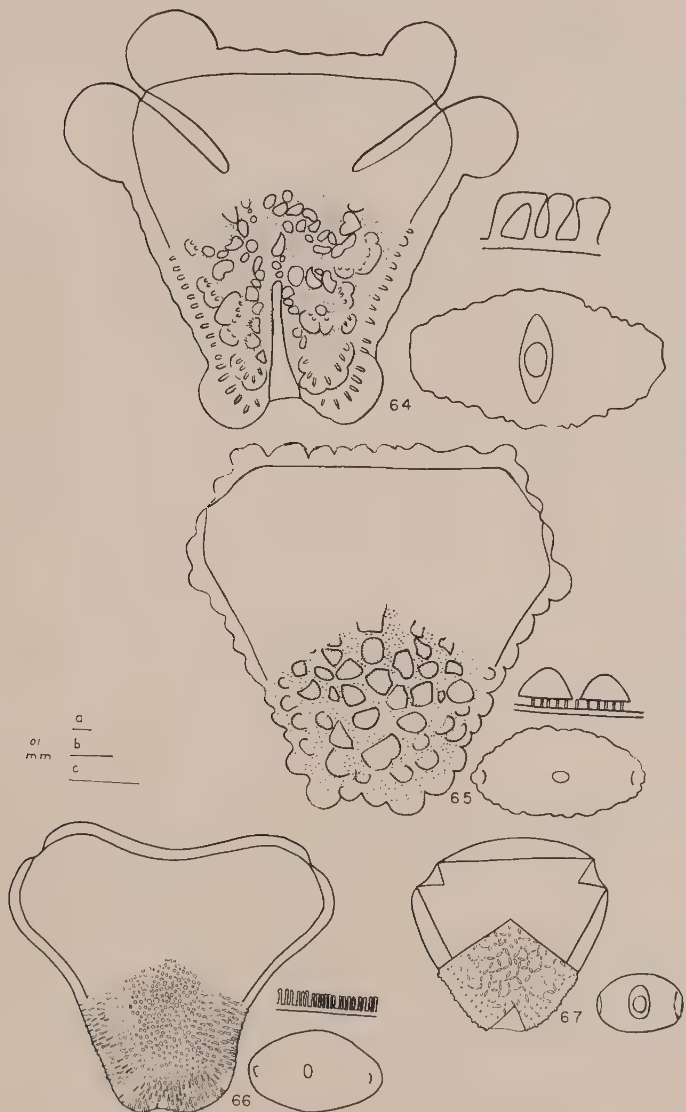


PLATE 6.—Palynograms of *Eperua* Aubl.—64. *Eperua falcata* Aubl., *B. W. 4791* (*MO*).—65. *Eperua rubiginosa* Miq., *B. W. 725* (*MO*).—66. *Eperua grandiflora* (Aubl.) Benth., *Steyermark 75537* (*NY*).—67. *Eperua campestris* Ducke, *Ducke 23291* (*US*).

a—magnification of the grain shown in the lower right corner.
b—magnification of the main figure.
c—magnification of LO and section of exine

Oblate spheroidal, $65 \times 69\ \mu$, (P/E = 0.99), lumina $14.4\ \mu$, muri $3.8\ \mu$.

Palovea Aubl.—Grains are 3-colporate, shape prolate spheroidal, ora spherical, narrow colpi, sexine verrucate, verrucae mostly spherical, interspaces granulate, warts supported by bacula, verrucae 6.8 to $8.2\ \mu$, sexine = 3× nexine.

Palovea brasiliensis Ducke, *Ducke 10882* (*NY*)—Plate 4, 47.
Suboblate, $46 \times 53\ \mu$, (P/E = 0.87), verrucae measuring $8.2\ \mu$ found only along the colpi margins, minute verrucae found on the remainder of the surface.

Palovea riparia Pulle, *Cowan 38814* (*NY*)—Plate 4, 45.
Prolate spheroidal, $61 \times 60\ \mu$, (P/E = 1.02), verrucae measuring $6.8\ \mu$ distributed equally over the grain surface.

Peltogyne Vog.—Grains are 3-colporate, shape varying from suboblate, to prolate spheroidal, or oblate spheroidal, ora lalongate to somewhat sperhical, sexine verucate to psilate with interspecific variation in the height of the bacula supporting the psilate tegillum, crassimarginate in some.

Peltogyne angustifolia Ducke, *Ducke* and *Kuhlmann 188* (*US*).
Suboblate, $36 \times 42\ \mu$, (P/E = 0.87), verrucae with crassimarginate condition.

Peltogyne campestris Ducke, *Ducke 17279* (*US*).
Suboblate, $37 \times 44\ \mu$, (P/E = 0.85), verrucate sexine, crassimarginate.

Peltogyne confertolia Benth., *Macedo 477*.
Suboblate, $39 \times 47\ \mu$, (P/E = 0.85), verrucate sexine, crassimarginate.

Peltogyne densiflora Spr. ex Benth., *Ducke 23275* (*NY*)—Plate 4, 48.
Suboblate, $38 \times 48\ \mu$, (P/E = 0.79), verrucate sexine, crassimarginate.

Peltogyne floribunda (H. B. K.) Benth., *Ducke 331* (*NY*)—Plate 5, 51.
Prolate spheroidal, $33 \times 27\ \mu$, (P/E = 1.01), psilate sexine, tegillum supported by densely spaced bacula, sexine = 6× nexine.

P. floribunda, *Ducke 518* (*US*).
Oblate spheroidal, $29 \times 31\ \mu$, (P/E = 0.92), sexine as in the above species.

Peltogyne glaziovii (Taub.) Dwyer, *Glaziov 13725* (*F*).
Oblate spheroidal, $24 \times 26\ \mu$, (P/E = 0.92), psilate to reticulate tegillum supported by densely spaced bacula, sexine = 2–3× nexine.

Peltogyne gracilipes Ducke, *Ducke 35181*.
Oblate spheroidal, $33 \times 34\ \mu$, (P/E = 0.98), psilate tegillum supported by long bacula.

Peltogyne lecointei Ducke, *Le Cointe s. n.* (*US*).
Suboblate, $37 \times 43\ \mu$, (P/E = 0.87), psilate sexine with short bacula.

Peltogyne maranhensis Huber ex Ducke, *Ducke 960* (*NY*).
Suboblate, $41 \times 47\ \mu$, (P/E = 0.87), verrucate sexine, crassimarginate.

Peltogyne micrantha Ducke, *Ducke 35090* (*US*).
Oblate spheroidal, $28 \times 32\ \mu$, (P/E = 0.90), verrucate sexine, crassimarginate.

Peltogyne paniculata Benth., *Ducke 35029* (*US*).

Suboblate, 24×28 μ, (P/E=0.88), verrucate sexine, crassimarginate.

Peltogyne paradoxica Ducke, *Ducke 17207* (*US*).

Suboblate, 32×37 μ, (P/E=0.88), psilate narrow sexine.

Peltogyne parvifolia Spruce ex Benth., *Williams 14406* (*MO*).

Oblate spheroidal, 28×31 μ, (P/E=0.90), psilate narrow sexine.

Peltogyne pubescens Benth., *Mutis 2376* (*US*).

Suboblate, 24×29 μ, (P/E=0.83), psilate narrow sexine.

P. pubescens, *Wurdack* and *Monachino 41224* (*NY*).

Suboblate, 26×30 μ, (P/E=0.88), psilate narrow sexine.

P. pubescens, *Schomburgk 791* (*NY*)—Plate 5, 54.

Suboblate, 24×29 μ, (P/E=0.88), psilate narrow sexine.

Peltogyne purpurea Pittier, *Allen 5593* (*US*).

Prolate spheroidal, 32×27 μ, (P/E=1.22), psilate tegillum supported by long densely packed bacula.

Peltogyne rigida Ducke, *Ducke 154* (*US*).

Suboblate, 40×49 μ, (P/E=0.83), verrucate sexine, crassimarginate.

Peltogyne venosa Benth., *Spruce s. n.* (*NY*).

Suboblate, 38×44 μ, (P/E=0.83), verrucate sexine, crassimarginate.

P. venosa, *Maguire 24951* (*U*).

Suboblate, 41×49 μ, (P/E=0.83), verrucate sexine, crassimarginate.

Saraca L.—Grains are 3-colporate, shape subprolate, long colpi, striate sexine, rounded amb.

Saraca declinata Miq., *Atchison 134*.

Subprolate, 41×32 μ, (P/E=1.29).

Schotia Jacq.—Grains are 3-colporate, shape prolate spheroidal and prolate, ora shape circular, rectangular or elliptical, sexine reticulate or striate, rounded amb.

Schotia brachypetala Sond., *Rodin 4534* (*US*).

Prolate spheroidal, 40×39 μ, (P/E=1.04), sexine reticulate.

Schotia humboldtioides Oliv., *Zenker 52* (*US*).

Prolate, 46×33 μ, (P/E=1.43), striate sexine.

Schotia speciosa Jacq., *Cummings* and *Wellington 223*.

Prolate spheroidal, 37×37 μ, (P/E=1.02), sexine reticulate.

Sindora Miq.—Grains are 3-colporate, shape suboblate, colpi broad, ora rectangular lalongate, sexine reticulate with very small lumina about 2 μ, long densely packed bacula with small capita, thick nexine ca. 1.5 μ, sexine=2× nexine, amb triangular with concave sides, grain diamond-shaped in equatorial view.

Sindora wallichii Graham ex Benth., *Ridley s. n.* (*F*) Plate 3, 38.

Suboblate, 48×55 μ, (P/E=0.86).

Tachigalia Aubl.—Grains are 3-colporate, shape suboblate to prolate spheroidal, being elliptical in equatorial view, colpi long narrow and psilate, ora shape predominately elliptical or rectangular lalongate, reticulate sexine with lumina size varying from ca. 1.9 to 3.9 μ, heterobrochate with polygonal lumina.

Tachigalia cavipes (Spruce ex Benth.) Macbr., *Schultes* and *Cabrera 12981* (*US*).

Suboblate, 32×38 μ, (P/E=0.86), lumina 3.5 μ.
Tachigalia formicarum Harms, *Ule 6538* (*MO*).
Suboblate, 23×28 μ, (P/E=0.83), lumina 1.9 μ.
Tachigalia multijuga Benth., *Riedel* and *Luschnath 125* (*NY*).
Suboblate, 31×36 μ, (P/E=0.86), lumina 2.1 μ.
Tachigalia myremecophila (Ducke) Ducke, *Huber 646* (*F*).
Suboblate, 24×30 μ, (P/E=0.81), lumina 2.1 μ.
Tachigalia paniculata var. *alba* (Ducke) Dwyer, *Ducke 932* (*US*).
Oblate spheroidal, 31×33 μ, (P/E=0.95), lumina 3.8 μ.
T. paniculata var. *alba*, *Krukoff 4633* (*US*).
Suboblate, 27×31 μ, (P/E=0.85), lumina 3.2 μ.
Tachigalia plumbea Ducke, *Maguire*, *Wurdack*, and *Keith 41769* (*US*).
Suboblate, 30×35 μ, (P/E=0.85), lumina 3.8 μ.
Tachigalia pubiflora Benth., *Anderson 752* (*US*)—Plate 3, 42.
Suboblate, 33×38 μ, (P/E=0.86), lumina 2.7 μ.
Tachigalia rigida Ducke, *Schultes* and *Lopez 9389* (*US*).
Suboblate, 28×32 μ, (P/E=0.88), lumina 3.1 μ.
Tachigalia rusbyi Harms, *Cardona 1654* (*US*).
Suboblate, 29×36 μ, (P/E=0.83), lumina 3.2 μ.
T. rusbyi, *Tutin 201* (*US*).
Suboblate, 27×31 μ, (P/E=0.86), lumina 3.1 μ.
Tachigalia schultesiana Dwyer, *Schultes* and *Cabrera 14045* (*MO*).
Oblate spheroidal, 29×32 μ, (P/E=0.90), lumina 2.4 μ.
Tachigalia tessmannii Harms, *Tessmann 4735* (*NY*).
Suboblate, 26×33 μ, (P/E=0.82), lumina 2.4 μ.
Tachigalia versicolor Standley and Williams, *Allen 5594* (*MO*).
Oblate spheroidal, 31×34 μ, (P/E=0.93), lumina 3.5 μ.
Tachigalia sp., *H. Garcia Borriga 13774* (*US*).
Suboblate, 27×33 μ, (P/E=0.83).

Tamarindus L.—Grains are 3-colporate, ora shape varying from spherical to lalongate, shape suboblate, colpi long and narrow, sexine rugulate, rounded amb.
Tamarindus indica, *Tonduz 7004* (*MO*).
Suboblate, 32*×38* μ, (P/E=0.85).

Tessmannia Harms—Grains are 3-colporate, shape suboblate, wide colpi, ora elliptical or rectangular lalongate, syncolpate, psilate tegillum supported by densely packed long bacula which increase in height about the ora margins giving the grain somewhat of an aspidote appearance, amb triangular with sides straight to concave, crassimarginate.
Tessmannia yangambiensis Louis ex J. Leonard, *Louis 10111* (*US*)—Plate 5, 49.
Suboblate, 33×41 μ, (P/E=0.82).

Trachylobium Hayne—Grains are 3-colporate, shape oblate spheroidal, long colpi, ora shape varying from rectangular to elliptical or spherical, snycolpate, or colpi not meeting at the poles, bacula supporting a psilate tegillum, sexine wider at the poles than in other regions, amb rounded.
Trachylobium verrucosum (Gaertn.) Oliv., *Schlieben 6240* (*MO*).
Oblate spheroidal, 30×33 μ, (P/E=0.90).
T. verrucosum, *Imperial Forestry Instit. Coll. 398*—Plate 5, 53.
Oblate spheroidal, 26×26 μ, (P/E=0.99).

KEY TO THE GENERA OF THE SCLEROLOBIEAE BASED ON POLLEN MORPHOLOGY
(acetolysed grains)

1. Sexine reticulate 2
1. Sexine not reticulate 9
  2. Grain width 17 μ .... *Poeppigia*
  3. Grain width > 17 μ 3
3. Grains united in permanent tetrads .... *Diptychandra*
3. Grains not united in permanent tetrads (*Sclerolobium albiflorum* excepted).. 4
  4. Grains of species occurring in either monads or tetrads ...... *Sclerolobium*
  4. Grains occurring in monads only 5
5. Psilate colpi with lalongate ora and lumina size ca. 1–3 μ 6
5. Clavate colpi with lolongate ora and lumina size greater than 3 μ .. *Cenostigma*
  6. Reticulate pattern very fine .... *Phyllocarpus*
  6. Reticulate pattern well defined 7
7. Lumina size ca. 3 μ .... *Melanoxylon*
7. Lumina size < 3 μ 8
  8. Grain width > 33 μ .... *Recordoxylon*
  8. Grain width < 33 μ .... *Vouacapoua*
    Batesia
9. Striate to rugulate or verrucate sexine .... *Dicymbe*
9. Psilate sexine .... *Campsiandra*

KEY TO SOME OF THE GENERA OF THE CYNOMETREAE BASED ON POLLEN CHARACTERS (acetolysed grains)

1. Grains possessing a polar axis > 30 μ 2
1. Grains possessing a polar axis < 30 μ 6
  2. Sexine striate 3
  2. Sexine not striate 4
3. Polar and equatorial axes > 45 μ .... *Neochevalierodendron*
3. Polar and equatorial axes < 45 μ .... *Hymenostegia*
  4. Sexine verrucate .... *Maniltoa*
  4. Sexine reticulate 5
5. Shape suboblate, ora elliptical lolongate, colpi wide and clavate ...... *Stahlia*
5. Shape prolate spheroidal, ora spherical, colpi narrow and psilate.... *Detarium*
  6. Sexine striate with narrow, haphazardly arranged lirae.... *Gilletiodendron*
    Aphanocalyx
    Cryptosepalum
    Scorodophloeus
    Plagiosiphon
    Talbotiella
    Monopetalanthus
    Cynometra
    (some African species)
  6. Sexine psilate 7
7. Shape subprolate .... *Pterogyne*
7. Shape other than subprolate 8
  8. Grain shape suboblate 9
  8. Grain shape prolate spheroidal to oblate spheroidal 10
9. Amb triangular with extended apices .... *Copaifera*
9. Amb triangular to rounded without extended apices .... *Guibourtia*
    Pseudocopaiva
  10. Sexine apparently perfectly smooth .... *Cynometra*
    (some species)
    Gossweilerodendron
    Oxystigma
  10. Sexine somewhat patterned surface 11
11. Sexine = nexine .... *Hardwickia*
    Kingiodendron
    Prioria
11. Sexine > nexine .... *Cynometra*
    (some species)

KEY TO SOME OF THE GENERA OF THE AMHERSTIEAE BASED ON POLLEN CHARACTERS (acetolysed grains)

1. Striate sexine 2
1. Striate sexine not present 5
 2. Lirae very narrow .... *Heterostemon*
 2. Lirae very broad 3
3. Sexine marked by fragmented and curved lirae .... *Amherstia* *Macrolobium*
3. Sexine marked by lirae in parallel arrangement running the entire length of the grain 4
 4. Polar axis of grains > 44 μ .... *Didelotia* *Berlinia*
 4. Polar axis of the grains < 44 μ .... *Crudia* *Oddoniodendron* *Saraca declinata*
5. Sexine rugulate 6
5. Sexine not rugulate 7
 6. Shape suboblate .... *Tamarindus*
 6. Shape oblate spheroidal .... *Lysidice*
7. Reticulate sculpturing 8
7. Reticulate sculpturing absent 17
 8. Lumina size from 7–18 μ, lumina surrounded by broad muri, lumina somewhat foveolate, fossapertuate 9
 8. Lumina size 8 μ, narrow muri, lumina polygonal, not fossapertuate 12
9. Grains 6-colporate and sometimes in tetrads .... *Afzelia*
9. Grains 3-colporate and in monads 10
 10. Grain surface uniformly reticulate 11
 10. Grains marked by coarsely reticulate mesocolpia and clavate apocolpia .... *Brachystegia*
11. Shape oblate spheroidal .... *Pahudia*
11. Shape prolate spheroidal .... *Intsia*
 12. Grain surface uniformly reticulate 13
 12. Grain surface not uniformly reticulate 16
13. Shape suboblate 14
13. Shape not suboblate 15
 14. Exine wide, diamond-shaped in equatorial view, tall bacula densely packed .... *Sindora*
 14. Sexine narrow, ellipsoidal in equatorial view, short bacula not densely packed .... *Tachigalia*
15. Polar axis > 40 μ .... *Schotia*
15. Polar axis < 40 μ .... *Hymenaea* *Brownea* (some species)
 16. Shape prolate or subprolate, long and narrow in equatorial view .. *Brownea* (some species)
 16. Shape suboblate, diamond-shaped in equatorial view .... *Baikiaea*
17. Retipilate sculpturing .... *Eperua* (*campestris* *oleifera* *purpurea*)
17. Retipilate sculpturing absent 18
 18. Ornate sculpturing .... *Eperua* *falcata*
 18. Ornate sculpturing absent 19
19. Verrucate sculpturing 20
19. Verrucate sculpturing absent 24
 20. Large prominent verrucae 21
 20. Small verrucae 23
21. Shape oblate .... *Eperua* (*leucantha* *rubiginosa*)
21. Shape other than oblate 22
 22. Distribution of verrucae uniform over the surface, oblate spheroidal, prolate spheroidal, or subprolate .... *Elizabetha* *Palovea riparia*

22. Distribution of verrucae only along the colpi margins, suboblate . . *Palovea brasiliensis*
23. Grains not crassimarginate . . . . *Brownea disepala*
23. Grains crassimarginate . . . . *Peltogyne* (some species)
24. Clavate baculate sculpturing . . . . *Eperua* (*grandiflora bijuga schomburgkiana*)
24. Psilate sexine 25
25. Sexine = 4–5 X nexine 26
25. Sexine = 2–3 X nexine 27
26. Grains syncolpate . . . . *Tessmannia*
26. Grains not syncolpate . . . . *Peltogyne* (some species)
27. Grains syncolpate . . . . *Trachylobium Hymenaea oblongifolia*
27. Grains not syncolpate 28
28. Polar axis > 30 μ . . . . *Daniella*
28. Polar axis < 30 μ 29
29. Grain length > 20 μ . . . . *Peltogyne* (some species)
29. Grain length < 20 μ . . . . *Hylodendron Crudia zenkeri*

INTERSPECIFIC RELATIONS

Dicymbe Spruce ex Benth.

Pollen from nine of the 12 species of *Dicymbe* was examined. Mature flowers of *D. corymbosa*, *D. bernardii*, and *D. yutajensis* were not available (Wurdack, personal communication) and hence were not included in the study.

The pollen of *Dicymbe* presents a wide range of shapes, sizes, and sexine patterns. These characters are illustrated in the pictorialized scatter diagram (Fig. 2). The sexine is marked by bacula supporting mural masses, which exhibit variation with a trend toward three types: those somewhat linear in form with parallel arrangement (striate), those elongate and narrow arranged haphazardly on the grain surface (rugulate), and those more or less isodiametric (verrucate) (Plate 1, 12, 13, 14).

Cowan (1957) divided the genus into four sections on the basis of the variability of petal number. Although these sections have already been invalidated by subsequent findings (Cowan, 1958), it is of interest to test palynological relationships with those indicated in the sections. In the pictorialized scatter diagram (Fig. 2) lines were drawn to enclose the genera of each section. The resulting picture clearly indicates that pollen characters do not delimit the sections. Rather, pollen characters thus far studied serve to add to the complexity of this genus.

Sclerolobium Vogel

Pollen of 36 specimens representing 30 species of *Sclerolobium* was examined. *Sclerolobium* has a somewhat uniform pollen type. All of the grains are 3-colporate with ora varying from rectangular to elliptical or spherical (Plate 1, 3, 9). Five shape classes were found among the pollen.

TABLE 1.—*Differences in Reticulate Sculpturing in Sclerolobium Pollen as Determined by Measurements of Lumen Size.*

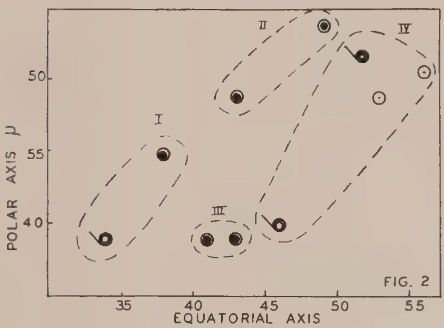
Species	Lumen size (in microns)			
	Reticulate		Subreticulate*	
	Range	Mean	Range	Mean
Section Oriens				
S. beaurepairei	(2.04–2.55),	2.3		
S. denudatum	(2.04–3.06),	2.7		
S. duckei	(2.55–3.57),	3.2		
S. fribrugense	(2.04–3.06),	3.0		
S. glaziovii	(2.04–3.06),	2.9		
S. rugosum	(1.53–3.06),	2.7		
S. subbullatum	(2.04–2.55),	2.1		
S. urbanianum	(2.04–2.55),	2.2		
Section Cosymbe				
S. aureum			0.51	
S. macropetalum			(1.53–3.06),	2.0
S. micropetalum			0.51	
Section Sclerolobiastrum				
S. melinonii			0.51	
Section Eusclerolobium				
S. albiflorum	(2.04–3.06),	2.8		
S. amplifolium	(2.55–3.57),	2.6		
S. chrysophyllum			(0.51–1.02),	1.3
S. densiflorum			(1.53–2.04),	1.3
S. eriopetalum			(1.02–2.04),	1.6
			1.0	
			1.0	
S. goeldianum			(0.51–2.55),	1.0
S. guianese			(1.53–2.55),	1.9
			(1.02–2.04),	1.6
			(1.53–2.55),	2.0
S. hypoleucum	(2.04–3.06),	2.4		
S. macrophyllum	(3.57–5.10),	4.1		
S. melanocarpum	(1.53–2.55),	2.3		
S. odoratissimum			(1.02–2.04),	1.3
S. paniculatum			(0.51–1.53),	1.0
S. paraense	(1.53–2.55),	2.2		
S. pilgerianum			(1.02–1.53),	1.0
S. rigidum			(0.51–1.02),	0.9
S. setiferum			(0.51–1.53),	1.0
S. striatum			(1.02–2.04),	1.5
S. tinctorium	(1.53–2.55),	2.2		

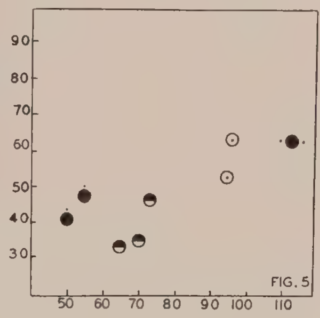
*The terms reticulate and subreticulate designate here two types of reticulum: reticulate, the lumen size varies from 2.0–4.1 μ; subreticulate, the lumen size varies from 2.0–<2.0 μ.

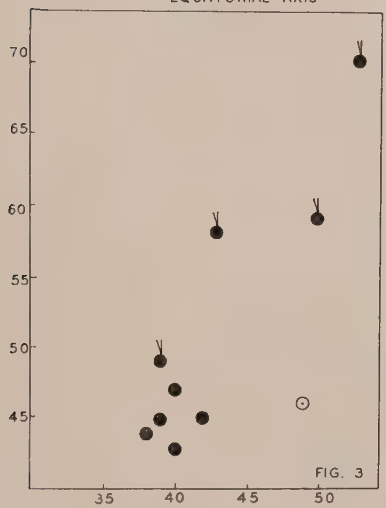
The species of the genus can be divided into two groups on the basis of the sexine: reticulate (lumen size 2.0–4.1 μ) and subreticulate (lumen size 2.0–<2.0 μ) grains (Table 1). The fact that the pollen of all of the species of section Oriens (Dwyer, 1957) is reticulate and that the pollen of 15 of the other species is subreticulate offers corroborative evidence for the establishment of this section.

Brownea Jacq.

The pollen of 11 specimens representing nine species of the New World genus *Brownea* was investigated. Three pollen types are differentiated on the basis of the pollen characters (Fig. 3). The first type is marked by coarse reticulation in the mesocolpia with diminution in lumen size towards the polar and colpi regions and a P/E range of 1.20–1.38 (Plate 3, 39). This type characterizes the species *B. leucantha*, *B. macbrideana*, *B. macrophylla*, and *B. rosa de Monte* and is concentrated in the upper two-thirds of the scatter diagram (Fig. 3).







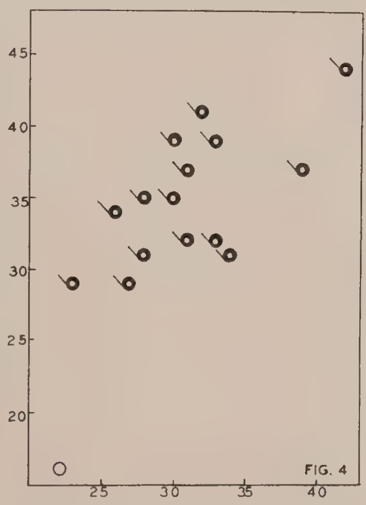


FIG. 2. Pictorialized scatter diagram representing variation in three pollen characters in 9 species of *Dicymbe* Spruce ex Benth. with reference to the sections established by Cowan (1957). I, section Eremopetala; II, section Apoxypetala; III, section Triplopetala; IV, section Dicymbe.

FIG. 3. Pictorialized scatter diagram representing variation in five pollen characters in 9 species of *Brownea* Jacq.

FIG. 4. Pictorialized scatter diagram representing variation in three pollen characters in 18 species of *Crudia* Schreb.

FIG. 5. Pictorialized scatter diagram representing variation in three pollen characters in 8 species of *Eperua* Aubl.

The second type, characterizing *B. grandiceps*, *B. similis*, *B. longipedicellata*, and *B. latifolia* falls in the lower left corner of the diagram. It is marked by a uniform reticulate pattern, and by a smaller P and E value than types one and three, respectively.

The third type having a P/E ratio different from the other two falls in the lower right quadrant. This type differs radically from the other two in the possession of a verrucate sexine and marks only one species of those studied, *B. disepala* (Plate 4, 46). Little (1948) notes the singularity of *B. disepala* in possessing white flowers borne in clusters on the trunks. Most species of *Brownea* have red flowers borne in terminal inflorescences.

Crudia Schreb.

Pollen of 18 specimens representing 18 species of the genus *Crudia* was studied. All of the grains are striate except those of *C. zenkeri* which are psilate. *C. zenkeri* is further differentiated by a much smaller polar axis and an oblate shape (Plate 5, 51). The striate type is uniform in sculpturing with narrow, unfragmented lirae arranged in parallel rows (Plate 5, 61). Although very uniform in the sexine pattern the striate grains possess five different shape classes: suboblate, oblate spheroidal, prolate spheroidal, subprolate, and prolate.

Syncolpate grains mark *C. reticulata* and *C. amazonica*.

Eperua Aubl.

The pollen of nine species of *Eperua* was investigated. Greater variation is found among the pollen of *Eperua* than any other genus studied.

Despite the striking variability, the grains are similar in shape being either oblate or suboblate with an angulapertuate amb. In some types the sides are strongly concave so that the apices are extended.

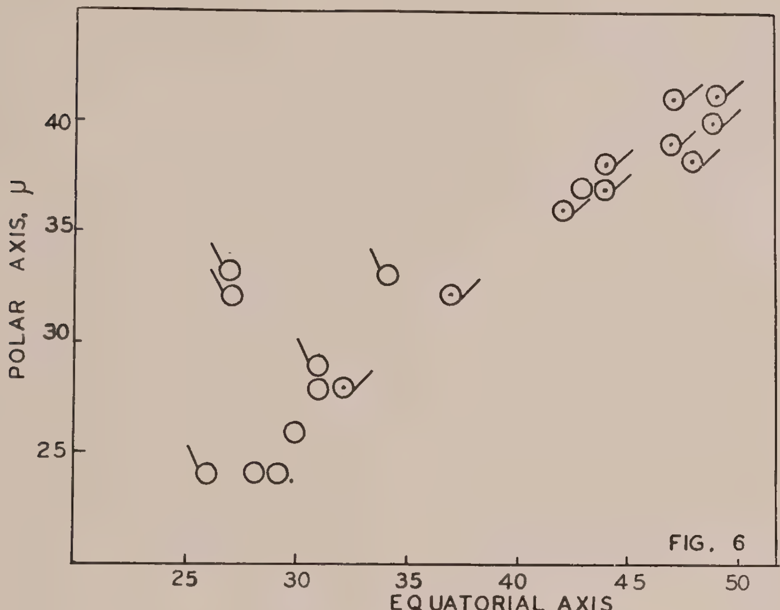
Great variation occurs in the length of the equatorial axis. Grain width has a range of 50 to 113 μ. This range is greater than the entire width range found in all the other pollen types of the three tribes (Fig. 15).

Four distinct types of sculpturing characterize the pollen of nine species: retipilate, verrucate, clavate baculate, and ornate (Plate 6). Palynologically the species are delimited into four groups (Fig. 5). The types will be discussed from left to right as they occur on the diagram and for convenience will be termed types one to four.

The first type characterizes three species, *E. campestris*, *E. oleifera*, and *E. purpurea* (Plate 6, 67). *E. purpurea* is not indicated on the graph since the distorted condition of the grains did not permit measurements. However, general similarity in size and in the retipilate sexine readily links it to this group. The grains vary in width from 50–54 μ and are distinctive in being suboblate in shape.

Ducke (1940) prepared a key to 11 species of *Eperua*. He indicated a close relationship between the above three species in the possession of a short non-pendulous inflorescence, stamens with filaments united basally into a short tube, and a glabrous ovary.

The second type characterizes three species: *E. bijuga*, *E. grandiflora*, and *E. shomburgkiana* (Plate 6, 66). A clavate baculate sculptur-



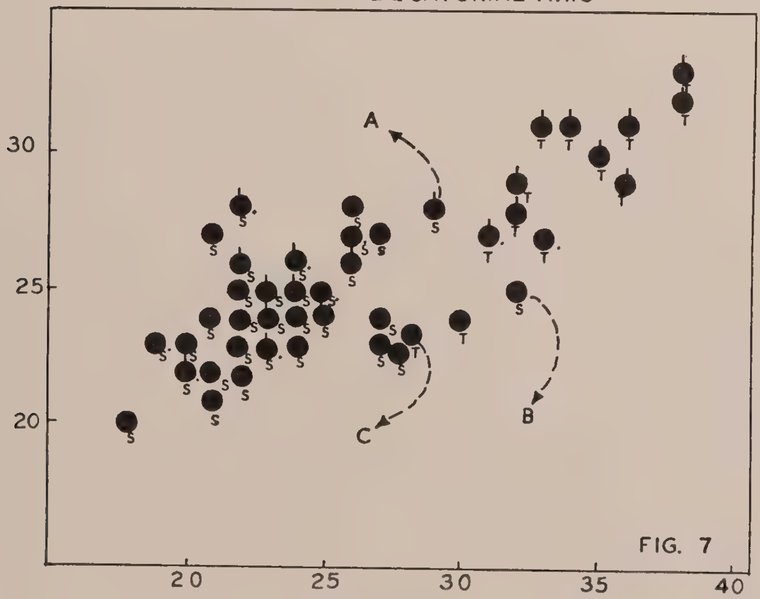


FIG. 6. Pictorialized scatter diagram representing variation in five pollen characters in 17 species of *Peltogyne* Vog.

FIG. 7. A palynological comparison of *Sclerolobium* (Sclerolobieae) and *Tachigalia* (Amherstieae) with respect to four pollen characters. (If two grains fell on the same point, one having a large lumen size and the other a small one, the large lumen size was indicated.) T, *Tachigalia;* S, *Sclerolobium;* A, *Sclerolobium macrophyllum;* B, *Sclerolobium melanocarpum;* C, *Tachigalia formicarum.*

ing, oblate shape, and a width range of 65–73 μ mark these grains. Ducke (1940) likewise noted their floral similarity in possessing much larger leaflets and flowers than the preceding species.

The third type characterized by verrucate sculpturing, an oblate shape, and a width range of 95–96 μ occurs in two genera, *E. leucantha* and *E. rubiginosa* (Plate 6, 65). The fourth type including at least one species, *E. falcata*, is unique and beautiful in the geometric precision of its design (Plate 6, 64). This type is oblate in shape, 3-colporate with brevicopi, and bears an ornate sexine. Erdtman (1952) describes the grain as being "coarsely reticulate (-ornate)." Admittedly the sexine could be described as reticulate since muri are separated by lumina. However, the term ornate which denotes an anastomosing of lumina seems to be more accurate and, used here, serves to emphasize the obvious difference between the reticuloid pattern found in the pollen of *E. falcata* and the reticulate pattern found in the other grains of the Amherstieae.

E. falcata, *E. rubiginosa*, and *E. leucantha*, the three species marked by the largest and most ornate pollen of types three and four, are characterized by very long pendulous inflorescences and tomentose ovaries. *E. falcata*, differentiated from the other two by ornate pollen, is distinguished florally in the possession of five fertile stamens. *E. rubiginosa* and *E. leucantha*, on the other hand, are marked by verrucate pollen and ten fertile stamens.

Peltogyne Vog.

The pollen of 21 specimens representing 17 species of the Central and South American genus *Peltogyne* was studied. Differences in shape and sexine pattern delimit three pollen types (Fig. 6). The first type falling near the lower left corner and characterized by a psilate tegillum supported by densely spaced long bacula and a P/E range of 0.88–1.15 marks *P. floribunda*, *P. gracilipes*, *P. purpurea*, and *P. glaziovii* (Plate 5, 52).

The pollen of *P. lecointei*, *P. paniculata*, and *P. pubescens* with a thin sexine and a P/E range of 0.75–0.88 constitutes the second type (Plate 5, 55). The pollen of the remaining species studied is marked by a verrucate sexine, a crassimarginate condition and a P/E range of 0.75–0.88, and constitutes the third type (Plate 4, 48).

The relationship between the pollen types is indicated in the pictorialized scatter diagram (Fig. 6). Types two and three fall in a line extending diagonally across the diagram, and are almost the same in shape with the third type being a little larger. Type one, which is above the diagonal, differs radically from them in shape and sexine pattern.

Ducke (1938) proposed a key for 14 species of *Peltogyne* of Brazilian Amazonia. The relationships proposed by him are partially substantiated by this study. *P. paniculata* and *P. pubescens*, both related palynologically, are related florally in possessing a calyx stipe and petals more or less oblong obovate or oblong spatulate and palynologically in the possession of type three pollen.

Ducke (1938) notes likewise the close similarity between *P. floribunda* and *P. gracilipes* florally in possessing very insignificant calyces

and bearing small flowers in lateral panicles. These two species are related palynologically in the possession of the first type of pollen.

Tachigalia Aubl.

Pollen of 15 specimens representing 14 species of *Tachigalia* was investigated. The study revealed a homogeneous group of grains.

The grains are all 3-colporate with lalongate ora and bear a reticulate sexine (Plate 3, 42). Lumen size varies from 1.9–4.0 μ. The grains are predominately suboblate in shape presenting a small P/E range from 0.81–0.95.

Several notes in the literature indicate a close relationship between *Sclerolobium*, the type genus of the Sclerolobieae, and *Tachigalia* traditionally placed in the Amherstieae. Baillon (1870, p. 115) says of *Tachigalia*, "Avec l'insertion ovarienne que caractérise le groupe des Amherstiées, ces plantes ont en même temps presque toute l'organisation florale des *Sclerolobium*, dont le gynécée est central, et servent, par conséquent, de lien entre les deux séries." Macbride (1943) says of it, "Nearly *Sclerolobium* except for the oblique calyx and the adnate stipe of the ovary." Dwyer (1954b), noting the great similarity between the two genera, suggests including *Sclerolobium* in the tribe Amherstieae. He points out that an additional character, myrmecodomatia of the foliage, shared by species of the two genera, seems to suggest close relationship.

The pictorialized scatter diagram (Fig. 7) indicates that palynologically *Sclerolobium* and *Tachigalia* are closely related, though distinct genera. The pollen of the two is similar in bearing a like heterobrochate reticulate sexine with polygonal lumina and in being 3-colporate with predominately lalongate ora; but differs in shape, size, and in the lumen size of the reticulum. Even in these characters there is slight intergeneric overlapping (Fig. 7).

Fifteen species of *Sclerolobium* share the large lumen size ($>2.0\ \mu$) with the species of *Tachigalia*. Only one species of *Tachigalia*, *T. formicarum*, is like the sclerolobiums in possessing small lumen size ($<2.0\ \mu$). Intergeneric overlapping in size of grains is also exhibited by *T. formicarum*. This species of all of the species of *Tachigalia*, palynologically is most closely related to the sclerolobiums (Fig. 7). Dwyer (1954b) using floral characters noted this relationship, stating in his monograph of *Tachigalia*, "One species, *T. formicarum* Harms, is not readily separated from *Sclerolobium* . . ." However, *T. formicarum* is typically tachigalian in the suboblate shape of its grains. The majority of the grains of *Sclerolobium* are oblate spheroidal or prolate spheroidal in shape. *Sclerolobium macrophyllum* and *S. melanocarpum* palynologically are most closely related to *Tachigalia* of all of the species of *Sclerolobium* (Fig. 7).

While *Tachigalia* palynologically is not related to the Amherstieae, it shows a close relationship to the genera of the Sclerolobieae which are marked by a reticulate sexine. It would appear from the present data—both floral and palynological—that *Tachigalia* belongs in the tribe Sclerolobieae even though it does possess an eccentric stipe, a character considered by some to be the key character of the tribe Amherstieae.

INTERGENERIC RELATIONS

Sclerolobieae

The pollen of 78 specimens representing 11 genera and 56 species of the tribe Sclerolobieae was investigated.

The various pollen types found in the Sclerolobieae are depicted in the pictorialized scatter diagram (Fig. 8). One basic pollen type predominates. It is marked by a reticulate sexine with some variation in lumen size, three narrow psilate colpi, a prolate spheroidal or oblate spheroidal shape, and lalongate ora. This basic type marks *Sclerolobium, Melanoxylon, Recordoxylon, Batesia, Vouacapoua, Phyllocarpus,* and *Poeppigia* (Plate 1). Florally as well as palynologically the first five genera represent a closely knit group of genera. *Phyllocarpus* is striking in the fineness of the reticulate sculpturing and *Poeppigia* in the narrowness of its grains (Plate 1, 4, 10). These two genera have been assigned to individual tribes, Poeppigiae and Phyllocarpieae, by Britton and Rose (1930). Although floral characters segregate the two genera from the tribe, the structure of the pollen does not *per se* warrant segregation from the tribe since the pollen is marked by reticulate sculpturing, the character marking the basic pollen type of the tribe.

Diptychandra shares the characteristic reticulate sculpturing but varies in being borne in tetrads (Plate 1, 5). *Diptychandra* is not depicted in Fig. 8 since the tetrahedral arrangement of the grains did not permit their individual measurement. *Sclerolobium albiflorum* also has tetrad pollen. This character may indicate relationship between the two genera. It is interesting to note that monads, dyads, and tetrads are found in the pollen of the Mimosaceae the subfamily closely related to the Caesalpiniaceae (F. G. Smith, 1956 and Erdtman, 1954).

Campsiandra differs from the basic type in possessing a psilate sexine entirely devoid of sculpturing (Plate 1, 2), but differs little in size and shape (Fig. 8). It deviates florally as well as palynologically from the other genera by possessing 15 to 20 stamens instead of the characteristic number of ten. Other floral characters suggest close relationship such as the presence of small bracteoles, five free and imbricate sepals, and five free petals.

The pollen of *Dicymbe* varies inter-specifically in sculpturing, shape, and size (Plate 1, 12, 13, 14). Three sexine patterns, rugulate, striate,

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EXPLANATION OF FIGURES

FIG. 8. Pictorialized scatter diagram representing the range of pollen characters in 11 genera including 56 species of the Sclerolobieae. B, *Batesia;* C, *Campsiandra;* CE, *Cenostigma;* D, *Dicymbe;* M, *Melanoxylon;* P, *Phyllocarpus;* PO, *Poeppigia;* R, *Recordoxylon;* S, *Sclerolobium;* V, *Vouacapoua.*

FIG. 9. Pictorialized scatter diagram representing the range of pollen characters in 22 genera including 52 species of the Cynometreae. A, *Aphanocalyx;* CO, *Copaifera;* CR, *Cryptosepalum;* CY, *Cynometra;* DE, *Detarium;* GI, *Gilletiodendron;* GU, *Guibourtia;* GO, *Gossweilerodendron;* HA, *Hardwickia;* H, *Hymenostegia;* K, *Kingiodendron;* M, *Maniltoa;* MO, *Monopetalanthus;* N, *Neochevalierodendron;* O, *Oxystigma;* PL, *Plagiosiphon;* P, *Prioria;* PS, *Pseudocopaiva;* PT, *Pterogyne;* SC, *Scorodophloeus;* ST, *Stahlia;* TO, *Talbotiella.*

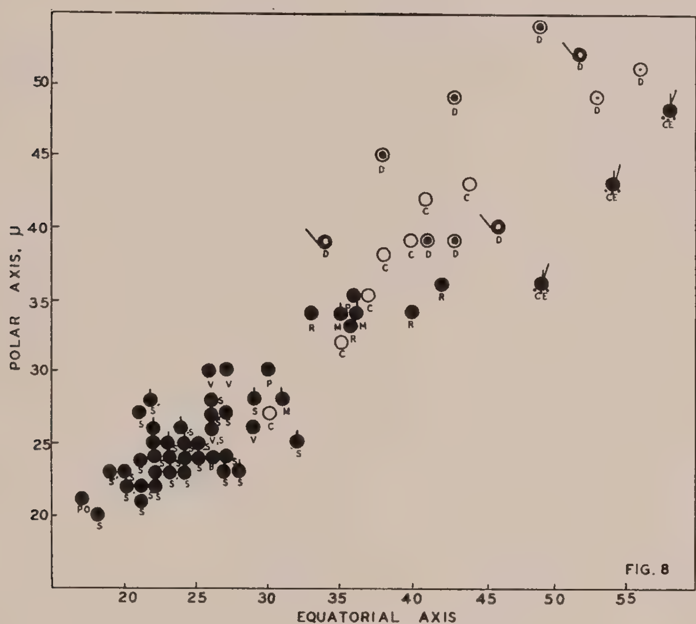
POLAR AXIS, μ
20
25
30
35
40
45
50
55
EQUATORIAL AXIS

FIG. 8

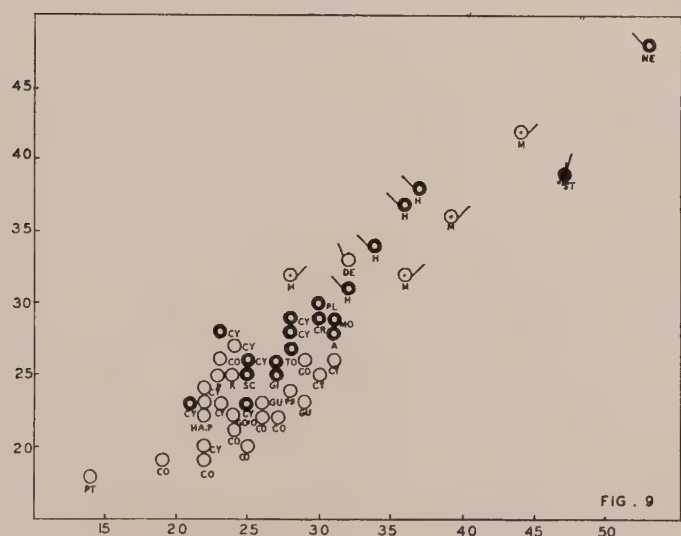
15
20
25
30
35
40
45
50

FIG. 9

and verrucate are represented (Fig. 8). That the pollen of *Dicymbe* is foreign to the Sclerolobieae is not surprising since the position of this genus in the tribe is highly controversial.

Ducke (1947) noted the close relationship of *Dicymbe* to the Amherstieae and pointed out that although the first three species described, *D. corymbosa*, *D. jenmani*, and *D. altsoni*, are marked by free and central insertion of the ovary (a characteristic of the Sclerolobieae), species more recently added, *D. amazonica*, *D. froesii*, and *D. heteroxylon*, are marked by a free but eccentric ovary or an ovary adnate to the wall of the receptacle (a characteristic of the Amherstieae). Later Ducke (1950) established a new genus *Dicymbopsis* for the latter two species. He remarked that the real affinity of these two species is with those genera of the Amherstieae marked by persistent bracteoles and strongly irregular flowers such as *Berlinia* and others of Western Africa. Cowan (1957 and 1958) did not discuss tribal relations in his study of *Dicymbe* but noted in the specific descriptions of *D. yutajensis*, *D. uaeparuensis*, and *D. altsoni*, "stipite ad hypanthii murum adnatum."

The verrucate, rugulate, and striate pollen, which marks *Dicymbe*, though lacking in the Sclerolobieae, is strongly represented among the pollen of the Amherstieae. Hence both floral and palynological characters indicate that *Dicymbe* while estranged from the Cynometreae has close affinity to the Amherstieae.

Cenostigma also has pollen grains clearly distinct from those of the other Sclerolobieae (Fig. 8). The pollen is marked by reticulate sculpturing, is of a suboblate shape, and bears wide clavate colpi possessing distinct lolongate ora (Plate 1, 11). Historically *Cenostigma* was segregated from the Sclerolobieae by Baillon (1870) and made a section of the genus *Caesalpinia* (Eucaesalpiniaceae). Hence an investigation of the pollen of five species of *Caesalpinia* was carried out: *Caesalpinia epunctata* (Ramos 48968 MO), *Caesalpinia coriaria* (Broadway 6295 MO), *Caesalpinia ruga* (Wenzel 1638 MO), *Caesalpinia mexicana* (Pringle 9724 MO), and *Caesalpinia exostemma* (Bartlett 293 MO). The pollen proved to be indistinguishable from that of *Cenostigma* in basic characters. This similarity of the pollen of *Cenostigma* and *Caesalpinia* offers supportive evidence for Baillon's (1870) contention of the close relationship between the two genera. He indicated that *Cenostigma* has "le périanthe et l'androcée des véritable Caesalpinia . . ."

Cynometreae

Pollen of 56 specimens representing 22 genera and 52 species of the Cynometreae was investigated. The pollen types found in the tribe are depicted in Fig. 9. Two basic types of pollen predominate: the finely striate and the psilate. Both types are marked by a small grain (polar axis $<30\ \mu$) and three narrow psilate colpi (Plate 2).

The finely striate type characterizes eight genera: *Aphanocalyx*, *Gilletiodendron*, *Cryptosepalum*, *Scorodopholoeus*, *Talbotiella*, *Plagiosiphon*, *Monopetalanthus*, and *Cynometra* (some African species). The placement of the genera *Cryptosepalum*, *Monopetalanthus*, and *Aphanocalyx* in the tribe has been highly controversial. Taxonomists have

reached no unanimity of opinion concerning the placement of these genera in the tribe Amherstieae or Cynometreae. Pollen characters may help to solve the enigma since they represent another character in favor of placement in the Cynometreae.

The second type or psilate type, tending to be smaller than the first type, characterizes ten genera: *Copaifera*, *Cynometra* (some species), *Gossweilerodendron*, *Hardwickia*, *Kingiodendron*, *Oxystigma*, *Prioria*, *Pterogyne*, *Guibourtia*, and *Pseudocopaiva*. Slight deviation from the psilate type occurs in *Hardwickia*, *Kingiodendron*, *Prioria*, and *Cynometra* (some species) in the acquisition of a somewhat patterned surface. The pollen of *Guibourtia*, *Pseudocopaiva*, and *Copaifera* (some species) is distinctive in being suboblate in shape. The close relationship between *Guibourtia* and *Pseudocopaiva* has long been recognized through studies of floral morphology. *Copaifera* is unique in possessing a triangular amb with extended apices. The psilate pollen type occurring in these genera indicates a close relationship in this group of genera as indicated by taxonomists who have studied gross characters (Baillon, 1870; Dwyer, 1954a; Capitaine, 1912).

Striate pollen of a different type marks the pollen of *Neochevalierodendron* and *Hymenostegia* (Plate 2, 33, 30). The pictorialized scatter diagram (Fig. 9) indicates that the pollen of these two genera differs in size as well as in sexine pattern from the two basic types. The lirae in the large pollen of *Neochevalierodendron* are broad, regular in shape, rarely fragmented, and arranged in exact parallel arrangement. The lirae of the somewhat smaller pollen of *Hymenostegia* are narrow but likewise tend to be unfragmented definite structures. These differentiating characters of *Hymenostegia* support its generic distinctiveness and its segregation from *Cynometra* to which it was at one time joined.

The pollen of *Neochevalierodendron* though vastly different from that found in the Cynometreae resembles the pollen of some of the genera of the Amherstieae where the striate types are larger, e.g. *Berlinia*. Another evidence of the relationship of this genus with the Amherstieae is the fact that formerly it had been included in *Macrolobium* (Amherstieae). It would seem that *Neochevalierodendron* rightly belongs to the Amherstieae although it was included in the Cynometreae by Leonard (1957) in his new definition of the tribes.

The pollen of *Stahlia* and *Maniltoa* are clearly distinct from the two basic types of pollen in the Cynometreae (Plate 2, 29, 23). The pictorialized scatter diagram (Fig. 9) indicates that *Stahlia* is segregated from the others by a reticulate sculpturing, wide clavate colpi, and elliptical lolongate ora. It resembles in all basic characters—shape, sexine pattern, clavate colpi, and lolongate ora—the pollen of *Cenostigma* and *Caesalpinia* investigated in this study. The fact that historically *Stahlia* was included in *Caesalpinia* (Britton, 1927) and that its pollen is similar to that of the latter genus would seem to indicate that there is some relationship between the two genera and in fact with *Cenostigma* (cf. p. 148.)

Maniltoa, possessing a radically different sexine pattern, a verrucate sexine, palynologically is not related to the genera of the Cynometreae (Plate 2, 29). Rather, the pollen of *Maniltoa* is nearly indistinguish-

able from that of *Peltogyne* of the Amherstieae. When in 1876 Scheffer described *Maniltoa* as a separate genus, he noted that it had some characters in common with the Amherstieae. "En outre notre *Maniltoa* possède encore quelques caractères, qu'on retrouve dans les genres du tribus des Amherstiées: La présence des stipules longues et étroites, qui tombent aussitôt que les bourgeons s'ouvrent; la présence d'un vrille droite, longue et raide, qui termine le petiole commun (comme c'est encore le cas dans les genres *Brownea*, *Humboldtia*, et *Amherstia*); la nature de l'inflorescence; es bractées . . ." Likewise Dwyer (1954a) in a preliminary key segregated some of the species of *Maniltoa* from *Cynometra* on the basis of the eccentric stipe of the ovary, a basic character of the Amherstieae. This study thus reveals another character that points to the affinity of *Maniltoa* with the Amherstieae rather than with the Cynometreae.

It is noteworthy that *Cynometra*, the type genus of the tribe, possesses pollen of both types. Perhaps more striking is the fact that the striate type was found to be restricted to African species alone. Other palynologists have noted that pollen characters may exhibit geographical distribution within a genus: Erdtman (1955) in *Macrolobium*; Coetzee (1955) in *Acacia* and Webster (1956) in *Phyllanthus*.

Amherstieae

Pollen grains of 115 specimens representing 28 genera and 104 species of the Amherstieae were investigated. Eight pollen types can be differentiated on the basis of the sexine pattern: striate, verrucate, reticulate, psilate, rugulate, baculate clavate, ornate, and retipilate. The last three types are confined to *Eperua*.

A pictorialized scatter diagram was constructed for each main pollen type, i.e. reticulate (Fig. 10), verrucate (Fig. 11), striate (Fig. 12), and psilate (Fig. 13) since any attempt to combine all four types on a single diagram resulted in a confusing picture. Rugulate is considered with the closely related striate type. The types represented in *Eperua* are not plotted in the individual type graphs but are included in the composite graph (Fig. 14) so that relationship of this genus to the tribe could be noted. Much overlapping occurs in the size and shape of the pollen of the various types so that together they represent a unified group with the exception of *Eperua* which falls almost entirely outside of the range of the pollen of the Amherstieae (Fig. 14).

The reticulate type plotted in Fig. 10 includes several different variations so diverse that they may not indicate relationships (Plate 3). Erdtman (1952, p. 21) noted this difficulty in the study of reticulate sexines, "A large reticulum, e. g. in the pollen of *Cobaea* may for instance not be strictly homologous with the fine reticulate patterns in many other plants."

The first type which is plotted in the upper right hand corner (Fig. 10) is marked by a coarsely reticulate sculpturing, brevicolpi, and a fossapertuate amb. This distinct type characterizes *Afzelia*, *Pahudia*, and *Intsia* (Plate 3, 35, 37, 34). Erdtman (1952) noted the similarity between the pollen of the first two genera. Pollen characters emphasize the close affinity between these genera, a relationship long recognized by taxonomists in the study of gross morphology (Bentham, 1865; Prain, 1901; Harms, 1915; De Wit, 1941; and Dwyer, 1954a).

The pollen of *Brachystegia*, though of a clearly unique reticulate type, is similar to the pollen of the above three genera (Plate 3, 36) in possessing a coarse reticulation, being fossapertuate, and having brevicolpi. The uniqueness of its pollen lies in the fact that the sculpturing of the apocolpia is different from that of the mesocolpia. This character was reported for three other species of *Brachystegia*—*B. spiciformis*, *B.*

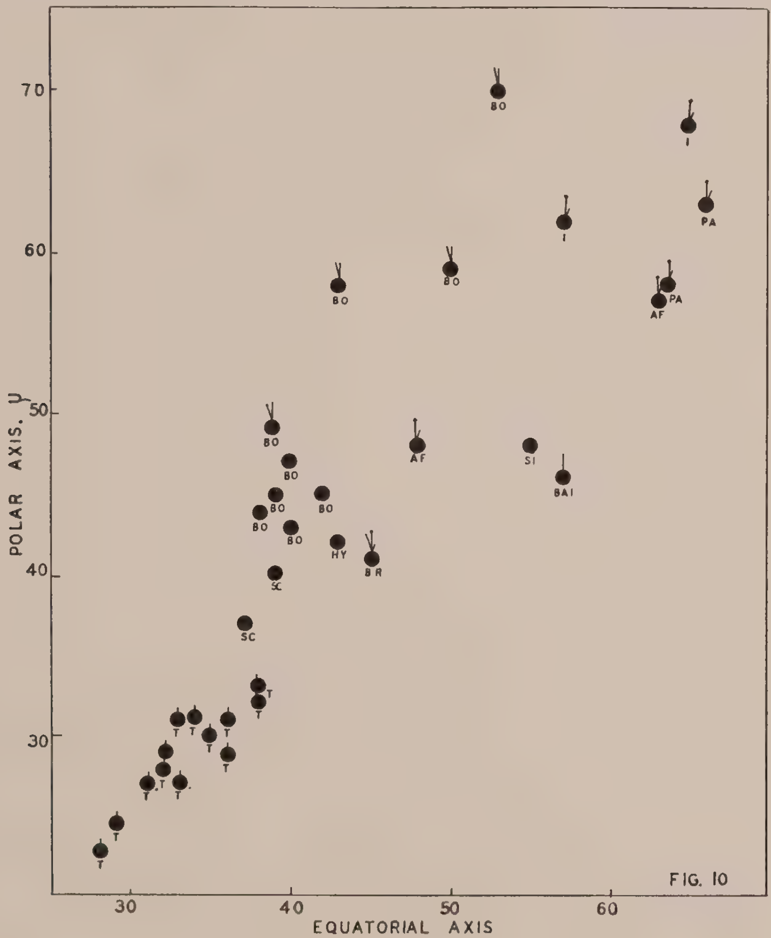

FIG. 10. Pictorialized scatter diagram representing the variation in reticulate grains among 10 genera of the Amherstieae. AF, *Afzelia;* BAI, *Baikiaea;* BR, *Brachystegia;* BO, *Brownea;* HY, *Hymenaea;* I, *Intsia;* PA, *Pahudia;* SC, *Schotia;* SI, *Sindora;* T, *Tachigalia.*

boehmii, and *B. longifolia*—by F. G. Smith (1956) in addition to the one reported for this paper.

The unique type of pollen characterizing *Brachystegia* offers supportive evidence of its distinctiveness as a genus. Leonard (1957,

p. 254)states of this African genus, "Genre homogène, bien distinct des genres voisins."

A reticulate sculpturing of an entirly different type marks the other genera in this group. *Baikiaea* and *Sindora* are isolated from other genera in the diagram (Fig. 10). Both are suboblate, diamond-shaped in equatorial view, of similar size, and bear distinct rectangular ora. They differ greatly, however, in the sculpturing. *Baikiaea* has a rather coarse and remarkably beautiful reticulation with lumina measuring ca. 8 μ (Plate 3, 40). *Sindora* is marked by a thick nexine with long bacula supporting small capita which fuse to form irregular tiny lumina (Plate 3, 38).

The pollen characters of *Baikiaea* give further evidence of its distinctiveness which was noted by Leonard in gross characters (1957, p. 74). He states, "Au point de vue structure de la fleur et du fruit, le genre se montre très homogène et bien différent des genres voisins."

Harms (1915) on the basis of gross morphological characters notes a striking resemblance between *Sindora* and *Tessmannia*. Palynologically they are similar in possessing a sexine marked by densely packed long bacula. *Tessmannia*, however, bears a psilate tegillum; whereas *Sindora* shows a slight reticulum.

There has been lack of agreement among taxonomists about the tribal allocation of *Sindora*. Bentham (1865) and Taubert (1892) placed it in the Cynometreae. Prain (1901) in noting this relationship remarks, "The very short calyx tube doubtless is in favor of this position . . . At the same time the stamens are not very suggestive of the tribe Cynometreae, while the fruit and seed would seem to indicate a greater affinity with Amherstieae." De Wit (1949) likewise notes, ". . . it is preferred to refer it to Amherstieae . . ." Pollen characters, too, favor its position in the Amherstieae.

Another pollen type is differentiated by a verrucate sculpturing (Fig. 11). The pollen grains of *Palovea*, *Elizabetha*, one species of *Brownea*, two species of *Eperua*, and several species of *Peltogyne* are verrucate (Plate 4). As is clearly indicated in the diagram (Fig. 11) the pollen of *Elizabetha* and *Palovea* is segregated from the remainder of the verrucate pollen by its larger size and more pronounced verrucae; whereas the pollen of *Peltogyne* is at the other extreme in possessing small verrucae and a small grain size. The grains of *Palovea brasiliensis* appear to represent an intermediate type. They are medium in size, simulate the large grains in bearing large verrucae, and the small in being crassimarginate (Plate 4, 47). The pollen of *Brownea disepala* approaches in size that of *P. brasiliensis* but differs in possessing small verrucae evenly distributed.

Pollen characters bear out the close relationship of *Brownea*, *Elizabetha*, and *Palovea*, a relationship recognized by students of floral morphology. Baillon (1870, p. 100) noted, "Les *Elizabetha* ont extérieurement tout à fait la fleur des *Palovea* . . ." He likewise notes an affinity between *Brownea* and *Elizabetha* as did Bentham (1865) and Capitaine (1912). Verrucate pollen of the small size and bearing small verrucae with the crassimarginate character marks 8 species of *Peltogyne*. This pollen is very similar to the pollen of *Maniltoa* (Cynometreae).

The most universal type of pollen is that marked by a coarse sculpturing (Fig. 12; Plate 5, 51–63). Eleven genera are marked by striate pollen: *Amherstia*, *Berlinia*, *Macrolobium*, *Didelotia*, *Saraca*, *Crudia*, *Heterostemon*, *Oddoniodendron*, and one species of *Schotia* as well as *Gilbertiodendron* and *Isoberlinia* described by Erdtman (1955) and F. G. Smith (1956), respectively. *Tamarindus* and *Lysidice* have a rugulate sculpturing believed to be closely related to the striate.

The striate pollen types tend to be extremely variable in size and shape and some even in the striations (Fig. 12). Nevertheless, it was possible to divide the striate pollen type into two basic types: those

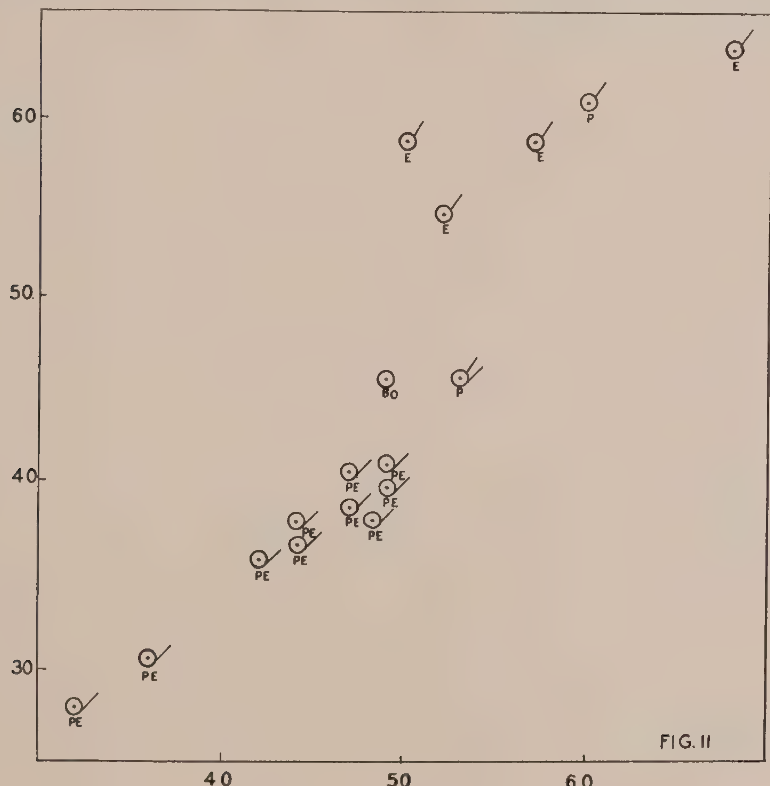

FIG. 11. Pictorialized scatter diagram representing the variation in verrucate grains among 4 genera of the Amherstieae. BO, *Brownea disepala*; E, *Elizabetha*; P, *Palovea*; PE, *Peltogyne*.

marked by regular lirae in parallel arrangement and those marked by fragmented and curved muri (fig. 12).

The striate character of *Heterostemon* differs radically from that marking the others by the possession of extremely fine lirae (Plate 5, 63). Erdtman's (1952) description of *Heterostemon ellipticus* does not concur with the findings of this study. He described the pollen of *H.*

ellipticus as being "psilate." The pollen of the species studied here as well as *H. mimosoides* (Ducke 768 US) appeared distinctly striate.

Erdtman (1952) describes the pollen of *Amherstia nobilis* as "striato-reticul(oid)ate." In the present investigation the sexine was rather variable from a striato-reticulate with a fragmenti- and curvimurate condition to an almost verrucate appearance.

A relationship between the genera marked by striate pollen has been recognized by taxonomists in the study of gross characters. Harms (1915) linked *Macrolobium* and *Berlinia*; and Baker (1930), the genera *Berlinia*, *Macrolobium*, and *Oddoniodendron*. Pellegrin (1948) in his key to the Leguminosae of Gabon linked the same three genera. Leonard (1957) indicated a close relationship between *Berlinia*, *Oddoniodendron*, *Isoberlinia*, and *Gilbertiodendron*.

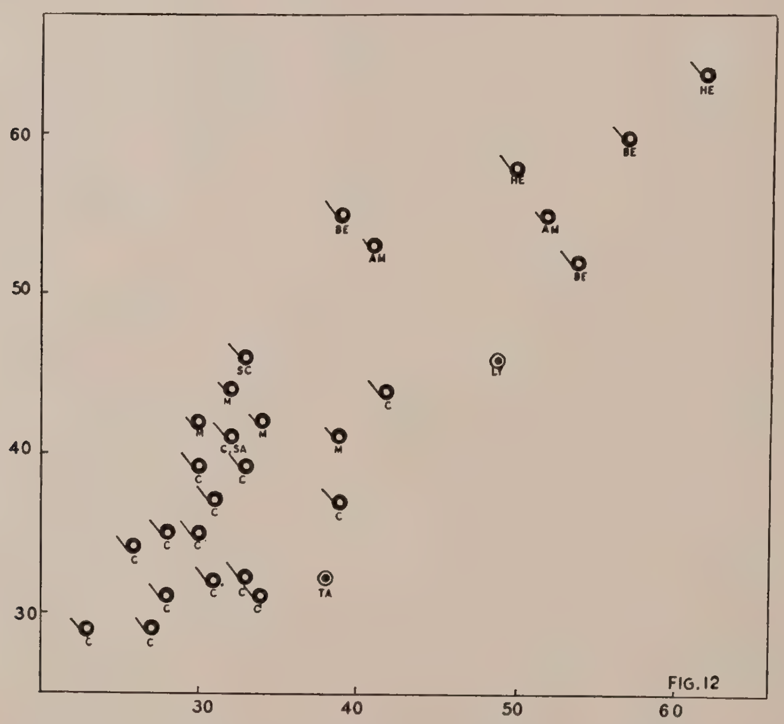

FIG. 12. Pictorialized scatter diagram representing the variation in striate grains among 10 genera of the Amherstieae; Am, *Amherstia:* BE, *Berlinia:* C, *Crudia:* HE, *Heterostemon:* LY, *Lysidice:* M, *Macrolobium:* OD, *Oddoniodendron:* SA, *Saraca declinata:* SC, *Schotia humboldtiodes:* TA, *Tamarindus*.

Originally *Crudia* was placed in the Cynometreae by Bentham (1840). In the revision of the tribes Bentham (1865) transferred it to the Amherstieae linking it with *Saraca*. Dwyer (1954a) likewise linked the two genera. Leonard (1957) placed it with the Cynometreae. Palynologically *Crudia* shows a distinct affinity to the Amherstieae with a close resemblance to *Saraca declinata*.

A psilate pollen type allows the delimitation of another pollen type illustrated in Fig. 13. This type characterizes *Trachylobium*, *Tessmannia*, *Hylodendron*, *Daniella*, *Crudia zenkeri*, and some species of *Peltogyne* (Plate 5, 49–56).

The pollen of *Hylodendron* and *Crudia zenkeri* are clearly segregated from the other pollen types by their small size (Fig. 13). The pollen of *Hylodendron* is very similar to that of the psilate type found in the Cynometreae. The grains are very small (polar axis $<16\ \mu$). Baker (1930, p. 772) notes the similarity between its fruit and that of *Gossweilerodendron* (Cynometreae), "Pod similar to those of *Gossweilerodendron* and *Pterygopodium*, with a membranous, winglike basal part, the seed being at the apex . . ." Harms (1915) likewise notes its relationship to the Cynometreae.

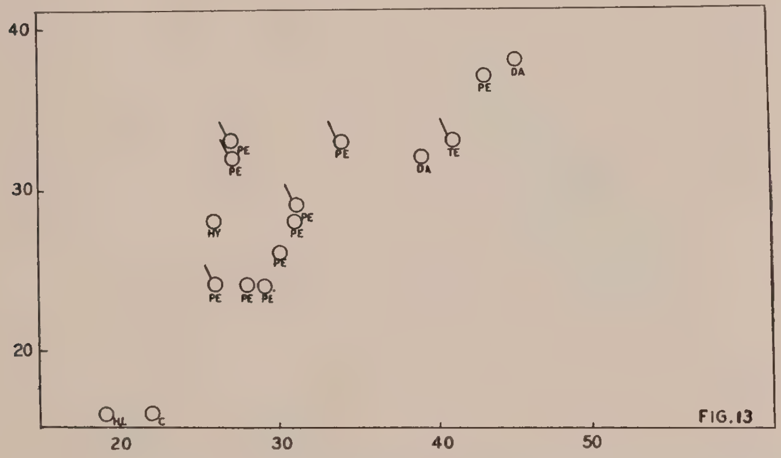

FIG. 13. Pictorialized scatter diagram representing the variation in psilate grains among 7 genera of the Amherstieae. C, *Crudia zenkeri:* DA, *Daniella:* HY, *Hymenaea oblongifolia:* HL, *Hylodendron:* PE, *Peltogyne:* TE, *Tessmannia:* TR, *Trachylobium.*

The pollen of *Trachylobium* is similar to that of *Hymenaea oblongifolium* (Plate 5, 53, 54). As indicated in the diagram (Fig. 13) they are nearly the same size. They both have a tendency to be syncolpate; they differ, however, in that the pollen of the former has increased in the width of the exine in the polar areas.

Daniella is very similar to some species of *Peltogyne* palynologically (Plate 5, 55, 56). Relationship among the genera marked by psilate pollen has been attested by taxonomists: Bentham (1865), Baillon (1870), Taubert (1892), and Macbride (1943).

The three pollen types not yet considered, the clavate baculate, retipilate, and ornate types, are found only in *Eperua* and are discussed under *Eperua* in "Interspecific Relations."

INTERTRIBAL RELATIONS

Pollen of 249 specimens representing 61 genera and 212 species of the tribes Amherstieae, Cynometreae, and Sclerolobieae was investi-

gated. Palynological data reveal, as noted above, certain generic relationships which support the transfer of some of the genera from one tribe to another. These transfers include the following: *Dicymbe* (Sclerolobieae) and *Neochevalierodendron* and *Maniltoa* (Cynometreae) to the Amherstieae as well as *Hylodendron* and *Tachigalia* (Amherstieae) to the Cynometreae and Sclerolobieae, respectively. These transfers recommended by floral morphological studies and strongly supported by palynological data are included in the scatter diagram in fig. 15 in which all three tribes are considered. *Cenostigma*, *Stahlia*, *Crudia zenkeri*, and *Eperua* do not appear to be palynologically related to any of the three tribes and hence are appropriately indicated. Otherwise it was not possible to indicate each genus because of the crowded condition of the symbols.

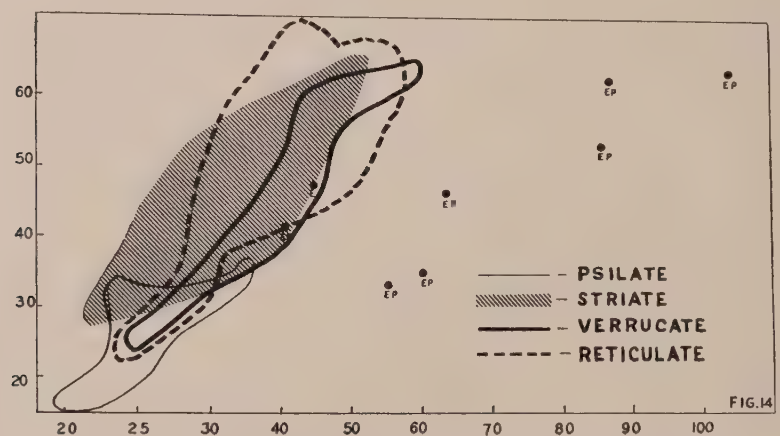

FIG. 14. Relationship of the four pollen types (verrucate, reticulate, striate, and psilate) in the Amherstieae. Ep, Eperua.

This diagram (Fig. 15) is an attempt to show intertribal relationships indicated through pollen studies. For example, a correlation seems to exist between attainment of large grain size and the acquisition of highly developed sculpturing. Because of this the location of the genera on the graph indicates not only the size and shape of the pollen but also the degree of sculpturing.

The wide expanse marked off by the pollen of the Amherstieae shows that their pollen is typically larger, more variable in shape, and somewhat more ornate then the pollen of the other two tribes. Overlapping in size occurs in the pollen of the Cynometreae and Sclerolobieae with the Cynometreae tending to be somewhat smaller. Despite the similarity in size of the two tribes, they are clearly delimited on the basis of sculpturing. Palynologically the three tribes are distinguished as discrete units. Thus pollen studies do not support Dwyer's suggestion (1954a) that the three tribes be united into a single large tribe. Rather pollen characters follow somewhat the same lines

as the character of fusion or non-fusion of the stipe of the ovary to the wall of the receptacle, the character originally used in defining the tribes. It is difficult to compare these findings with those of Leonard (1957) since he restricted his studies to African genera, the genera given least attention in this study. In general pollen characters do not seem to support the recently defined tribes.

Campo-Duplan (1947) found a correlation between increase in pollen size and a highly evolved type in the Abietineae. She (1949) likewise noted that advanced families tend to have a more ornate pollen than primitive ones. Accepting largeness and ornateness of grains as criteria of palynological advancement, it appears that the Amherstieae represent the most advanced of the tribes, whereas the Cynometreae are the most primitive.

The pollen of the Amherstieae, with the acquisition of a variety of ornamentations—verrucae, striae, clavae, rugulae, and a highly specialized reticulum—along with the attainment of large pollen size and a great variety of shapes, represents the most advanced pollen. The pollen of the Cynometreae, being not only the smallest but also possessing the simplest type of sexine (psilate to finely striate) is the least specialized. The Sclerolobieae appear to represent the intermediate type with the acquisition of a simple reticulate type of sculpturing and with pollen of a somewhat larger size than in the Cynometreae but smaller than the Amherstieae.

The scatter diagram serves well for a palynological phylogenetic scheme of the three tribes (Fig. 15). The pollen grains exhibit progressive advancement in pollen characters from left to right across the diagram. The simplest or psilate types are first, then the reticulate, the striate, verrucate, and finally the highly developed reticulate types found in *Afzelia*, *Intsia*, and *Pahudia*. *Eperua* representing the extremes in sculpturing characters, is located at the far right hand side of the diagram.

A survey of the pollen of these tribes shows a striking relation between the types of sculpturing and the geographic distribution of the genera. Such a relation was noted by Dahl (1952) in his study of the pollen of the Icacinaceae. He remarks, "Most of the New World genera are characterized by type A pollen."

All of the genera possessing grains marked by verrucae are New World genera: *Dicymbe*, *Maniltoa*, *Peltogyne*, *Brownea*, *Palovea*, *Elizabetha*, and *Eperua*. The striate type whether the finely striate type of the Cynometreae or the coarse type of the Amherstieae is almost entirely restricted to African or Asiatic genera; those in the Amherstieae are: *Berlinia*, *Macrolobium*, *Amherstia*, *Gilbertiodendron*, *Isoberlinia*, *Oddoniodendron*, *Neochevalierodendron*, *Didelotia*, *Lysidice*' *Tamarindus* (pantropical), and *Crudia* (pantropical); those in the Cynometreae are: *Plagiosiphon*, *Talbotiella*, *Gilletiodendron*, *Aphanocalyx*, *Cynometra* (African species), *Cryptosepalum*, *Monopetalanthus*, *Hymenostegia*, and *Scorodophloeus*. The only strictly American genera bearing striate pollen are *Dicymbe* and *Heterostemon* and, as noted earlier, the striate type of *Heterostemon* differs radically from the others. *Dicymbe* has not only striate but also verrucate pollen which tends to link it to the American genera.

The particular reticulate type characterizing the American tribe Sclerolobieae is restricted to American genera. The American genus *Tachigalia*, a member of the Amherstieae, is also marked by this type of reticulation.

FIG. 15. Comparison of the tribes Sclerolobieae, Cynometreae, and Amherstieae with respect to pollen characters with special reference to *Eperua*, *Cenostigma*, *Stahlia*, and *Crudia zenkeri*. (It was not possible to plot the pollen of every specimen because of the great amount of overlapping in size. An attempt was made to plot a representative sample of each tribe in the crowded areas.) EP, *Eperua:* St, *Stahlia:* CE, *Cenostigma:* CZ, *Crudia zenkeri*.

SUMMARY AND CONCLUSION

1. That palynological characters can be used to advantage in taxonomic studies is currently recognized and clearly evidenced by this investigation. Pollen characters investigated in this study of the pollen of 212 species of the Amherstieae, Cynometreae, and Sclerolobieae proved to be useful in delimiting higher plant groupings, i.e. tribes.

One basic pollen type, marked by a reticulate sexine, three narrow psilate colpi, and lalongate ora, predominates in the tribe Sclerolobieae. Two basic types of pollen characterize the tribe Cynometreae: those with a finely striate sexine and those with a psilate sexine. The two types are similar in possessing a small polar axis ($<30\ \mu$) and three narrow psilate colpi.

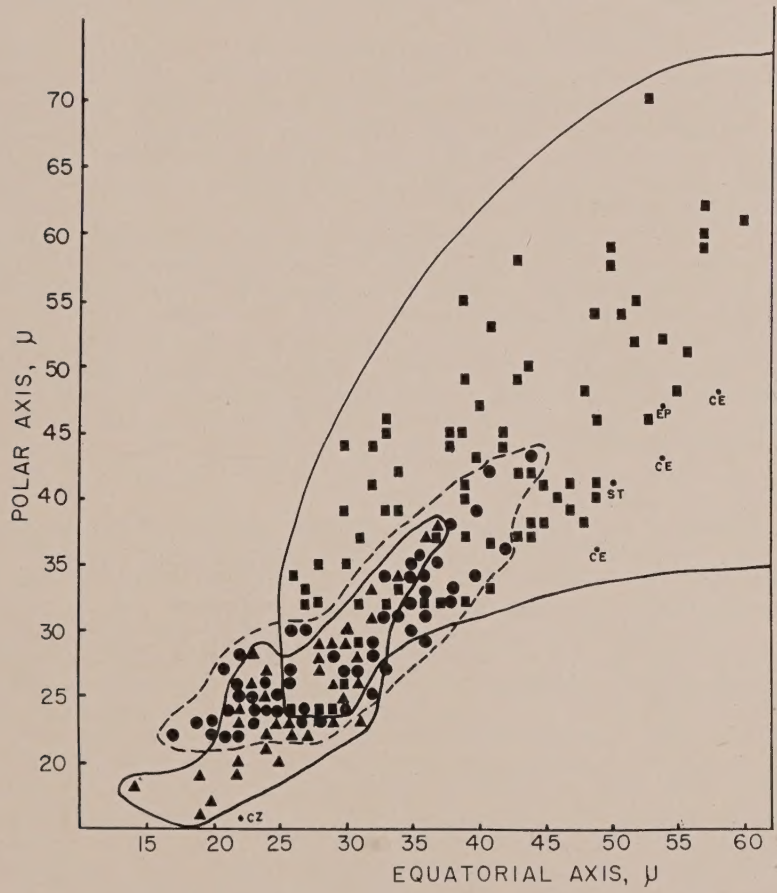

Fig. 15a. See *Gossweilerodendron balsamiferum* (Verm.) Harms, listed on page 120.

Four basic types, psilate, striate, reticulate, and verrucate, mark the tribe Amherstieae. In addition clavate baculate, retipilate, and ornate pollen are represented among the pollen of *Eperua* (Amherstieae).

2. The distinctiveness of the pollen characters within each tribe suggested certain transfers of genera from one tribe to another. The literature indicated that the genera, which were found to vary from the

characteristic pollen type in a tribe, usually also deviated in floral characters.

The transfers suggested by pollen characters and recommended by floral studies include: *Dicymbe* (Sclerolobieae) to the Amherstieae; *Maniltoa* and *Neochevalierodendron* (Cynometreae) to the Amherstieae; and *Hylodendron* and *Tachigalia* (Amherstieae) to the Cynometreae and Sclerolobieae, respectively. Strangely the pollen grains of *Cenostigma* (Sclerolobieae), *Stahlia* (Cynometreae), and *Caesalpinia* (Euscaesalpiniae) are nearly identical.

3. Pollen characters follow somewhat the same lines as the character of fusion or non-fusion of the ovary to the wall of the receptacle. Hence the tribes as delimited palynologically are much the same as the originally defined tribes (Bentham, 1865). Dwyer's (1954a) suggestion that the three tribes be united into one is not supported by this study; neither do Leonard's (1957) recently defined tribes appear to be supported by pollen characters.

4. In the intratribal investigation certain intergeneric relations were noted. Most of these relations had been suggested previously on the basis of floral morphology. In the Sclerolobieae, *Sclerolobium*, *Melanoxylon*, *Recordoxylon*, *Batesia*, and *Vouacapoua* represent a closely knit group of genera. In the Cynometreae the finely striate type of pollen links *Aphanocalyx*, *Gilletiodendron*, *Cryptosepalum*, *Scorodophloeus*, *Talbotiella*, *Plagiosiphon*, *Monopetalanthus*, and *Cynometra*. The psilate type marks *Copaifera*, *Gossweilerodendron*, *Hardwickia*, *Kingiodendron*, *Oxystigma*, *Prioria*, *Pterogyne*, *Guibourtia*, *Pseudocopaiva*, and *Cynometra*. Thus two palynologically defined groups are found in the Cynometreae.

Within the Amherstieae, *Afzelia*, *Pahudia*, and *Intsia* form a distinct group. *Palovea*, *Elizabetha*, and *Brownea; Peltogyne* (some species) and *Maniltoa; Trachylobium* and *Hymenaea;* and the group of genera characterized by striate pollen form distinct groups.

5. In addition to proving useful in delimiting the tribes and in noting certain generic relationships, pollen characters were also found to be useful in the recognition of certain interspecific relations. *Dicymbe*, *Brownea*, *Eperua*, and *Peltogyne* were found to be surprisingly variable palynologically. Pollen characters in *Eperua* and *Peltogyne* support the recognized relationships based on floral characters. Since no monographic study of *Brownea* has yet been carried out, it was impossible to compare palynological findings in this genus with other findings. The variability of the pollen of *Dicymbe* seems to add to the confusion of the genus. Other genera—*Sclerolobium*, *Crudia*, and *Tachigalia*—present very homogeneous pollen characters with little variation except for shape and size. However, it is noteworthy that the section Oriens of the genus *Sclerolobium* was delimited by lumen size of the reticulum.

Evidence was shown of the extremes to which pollen may advance within a single genus. The pollen of *Eperua* presents a greater width range than found in all the other pollen of the three tribes. In addition the three sculpturing patterns found in this genus are unique to it alone.

6. A striking relation was noted between pollen types and geographical distribution both within a genus and within a tribe. The

finely striate type in *Cynometra* is limited to African species. Tribally the verrucate type is limited to New World genera; the striate type, nearly without exception, to Old World genera.

7. Pictorialized scatter diagrams, based on a modification of Anderson's technique, were used in the palynological analysis. In this study they proved to be very efficient in portraying relationships among the pollen types in size, shape, ora, colpi, and sculpturing.

BIBLIOGRAPHY

Anderson, E. 1954. Efficient and Inefficient Methods of Measuring Specific Differences. Statistics and Mathematics in Biology. Edited by O. Kempthorne, T. A. Bancroft, J. W. Gowen, and J. L. Lush. Iowa State College Press, Ames, Iowa.

Baillon, H. 1870. Histoire des plantes, Librairie Hachette et C^ie^, Paris, **2**: 73–196.

Baker, E. G. 1930. The Leguminosae of Tropical Africa. Unitas Press, Ostend, 3.

Bentham, G. 1840. Contributions towards a Flora of South America.—Enumeration of Plants collected by Mr. Schomburgk in British Guiana (Suborder Caesalpinieae). Hooker's Journal of Botany. **2**: 72–103.

Bentham, G. and **Hooker, J. D.** 1865. Genera Plantarum. **1**(2): 562–600.

Britton, N. L. 1927. *Stahlia monosperma*. Addisonia. **12**(3): 33–34.

Britton, N. L. and **Rose, J. N.** 1930. Caesalpiniaceae. North American Flora. **32**(4): 201–269.

Campo-Duplan, M. Van. 1947. Considérations biométrique sur les grains de pollen des Abiétinées. Bull. Soc. Hist. Nat. Toulouse. **82**(3/4): 193–200.

———. 1949. Considérations générales sur l'évolution des grains de pollen. Bull. Soc. Hist. Nat. Toulouse. **84**(1/2): 33–41.

Capitaine, L. 1912. Étude Analytique et Phytogéographique de groupe des Légumineuses. Paul Lechevalier, Paris. 319–404.

Coetzee, J. A. 1955. The Morphology of *Acacia* pollen. South Afr. J. Sci. **52**: 23–27.

Cowan, R. S. 1957. Leguminosae-Caesalpinioideae in the Botany of the Guayana Highland, Part III. Mem. N. Y. Bot. Gard. **9**(3): 337–343.

———. 1958. Studies in Tropical American Leguminosae IV. Brittonia. **10**(1): 28–31.

Cranwell, L. M. 1953. New Zealand Pollen Studies—The Monocotyledons. Bull. Auckland Inst. and Mus. **3**.

Dahl, A. O. 1952. The Comparative Morphology of the Icacinaceae, IV. The Pollen. Jour. Arnold Arb. **33**: 252–286.

Ducke, A. 1938. Notes on the Purpleheart Trees (*Peltogyne* Vog.) of Brazilian Amazonia. Trop. Woods. **54**: 1–7.

———. 1940. Notes on the wallaba trees (*Eperua* Aubl.). Trop. Woods. **62**: 21–28.

———. 1947. New forest trees and climbers of the Amazon, Sixth series. Trop. Woods. **90**: 7–30.

———. 1950. Plantas no vas ou pouco conhecidas da Amazonia. (Notas sobre a flora neotropica III.). Bol. Téc. Inst. Agron. Belem. **19**: 1–42.

Dwyer, J. D. 1954a. Rapports entre stipe et coupe réceptaculaire dans la classification des Amherstieae (Caesalpiniaceae), 8^e^ Congrès Int. Bot., Paris, Rapp. et Comm. Sect. **4**: 52–54.

———. 1954b. The Tropical American Genus *Tachigalia* (Caesalpiniaceae). Ann. Missouri Bot. Gard. **41**: 223–260.

———. 1957. The Tropical American Genus *Sclerolobium* Vogel (Caesalpiniaceae). Lloydia. **20**(2): 67–118.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy I. Angiosperms. Chronica Botanica Co., Waltham, Mass.

———. 1954. Pollen Morphology and Plant Taxonomy. Bot. Not. **2**: 65–81.

———. 1955. Pollen Morphology and Plant Taxonomy in some African Plants. Webbia. **11**: 405–412.

———. 1957. Pollen and Spore Morphology/Plant Taxonomy II. Gymnospermae, Pteridophyta, Bryophyta. Ronald Press Co., New York.

Faegri, K. and **Iversen, J.** 1950. Textbook of Modern Pollen Analysis. Ejnar Munksgard, Copenhagen.

Harms, H. 1915. Caesalpinioideae. Die Pflanzenwelt Afrikas in Engler and Drude, Die Vegetation der Erde. 93(1): 423–520.
Leonard, J. 1957. Genera des Cynometreae et des Amherstieae Africaines (Leguminosae-Caesalpinioideae). Essai de blastogenie appliqués à la systematique. Mem. Acad. Roy. Belgique Cl. Sci. **30**(2): 1–307.
Little, E. L., Jr. 1948. New Species of trees from western Ecuador. Jour. Washington Acad. Sci. **38**(3): 87–105.
Macbride, F. J. 1943. Flora of Peru. Field Museum of Natural History-Botanical Series. **13**(3,n.1).
Pease, D. C. and **Baker, R. F.** 1948. Sectioning Technique for Electron Microscopy Using a Conventional Microtome. Proc. Soc. Exp. Biol. and Med. **67**: 470–474.
Pellegrin, F. 1948. Les Légumineuses du Gabon. Mem. Inst. Et. Centrafr. **1.**
Prain, D. 1901. On the Characters and Relationships of *Afzelia* (Smith). Scientific Memoirs by Medical Officers of Army of India. **13**: 33–49.
Scheffer, R. H. 1876. Énumération des plantes de la Nouvelle-Guinée, avec description des espèces nouvelles-Léguminosae. Ann. Jard. Bot. Buitenzorg. **1**: 17–23.
Smith, F. G. 1956. Bee Botany in Tanganyika. Unpublished Ph.D. dissertation, University of Aberdeen, Scotland.
Taubert, P. 1892. Caesalpinioidae. Engler and Prantl, Die Natürlichen Pflanzenfamilien. **3**(3): 125–184.
Tulasne, M. L. R. 1845. Légumineuses Arborescentes de l'Amérique de Sud. Archives du Museum d'Histoire Naturelle. **4**: 9–195.
Webster, G. L. 1956. A Monographic Study of the West Indian species of *Phyllanthus*. Jour. Arnold Arb. **37**: 217–268.
Wit, H. C. D. de. 1941. Notes on the genera *Intsia* and *Pahudia* (Legum.). Bull. Bot. Gard. Buitenzorg. **17**(1): 139–154.
———. 1949. The genus *Sindora* Miquel (Legum.). Bull. Bot. Gard. Buitenzorg. **18**(1): 5–82.
Wodehouse, R. P. 1928. Pollen Grains in the Identification and Classification of Plants II. *Barnadesia*. Bull. Torrey Club. **55**: 449–462.